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Project Quinte:
Point-Source Phosphorus Control and Ecosystem Response in the Bay of Quinte, Lake Ontario

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Foreword

This publication reports the findings of Project Quinte scientists over the period 1972–84 when phosphorus inputs from sewage treatment plants on the Bay of Quinte were high (1972–77) and when they were reduced (1978–84). Dramatic changes were found in the lower and higher trophic levels when phosphorus inputs were reduced, but changes in the intermediate trophic levels were minimal. The papers presented here document these results and offer interpretations of the data that fit the authors' models.

It is the belief of the Project Quinte group that our findings in the Bay of Quinte will have applications in other areas of the Great Lakes Basin. The results of other rehabilitation programs in the Great Lakes will provide a useful comparison to our own.

Project Quinte has been sustained by the continuing commitment of scientists and managers from the Ontario Ministry of Natural Resources, Ontario Ministry of the Environment, and the Department of Fisheries and Oceans. The Glenora Fisheries Station served as an important geographical and scientific focus throughout the project. The Project Quinte group expresses its appreciation of the efforts of the technical and clerical staff of the Station and of its scientist-in-charge, W. J. Christie.

This publication was assisted through its various stages by Ms. Johanna Reinhart, editor of the Scientific Information and Publications Branch, and the special editor, Dr. L. W. Billingsley, who was unfortunately unable to complete the task, and Dr. Philip E. K. Symons.

Abstract

Minns, C. K., D. A. Hurley, and K. H. Nicholls [ed.] 1986. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

The Bay of Quinte of Lake Ontario is a large (254 km^2) body of water with a variety of significant human uses including industrial and drinking water supply, wastewater disposal, recreational swimming, boating and angling, and commercial fishing. Scientists from federal and provincial government agencies and some Ontario universities collaborated between 1972 and 1985 to examine the effects in 1978 of significant reductions in phosphorus from municipal sewage treatment plants on abiotic and biotic features of the bay. Cultural impacts from land clearance since the early 1800s have overridden natural conditions in the bay by increasing phosphorus loads, and this has eventually had noticeable effects on some biotic assemblages. Because of increasing population and the widespread use of high-phosphorus detergents, phosphorus loading escalated after 1940. Water quality deteriorated in the 1950s and 1960s, seriously affecting municipal water supplies, recreational opportunities, and sport and commercial fisheries. Increasing phytoplankton abundance decreased light penetration and, in turn, reduced the abundance of submerged macrophytes after the 1950s. By the 1970s these plants were limited to the shallow euphotic zone of less than 2 m in the upper bay and 4 m in the lower bay. During the late 1960s and early 1970s the production rates and biomass of phytoplankton and zooplankton were among the highest recorded in natural freshwater. In the most eutrophic section of the bay, total phosphorus concentrations averaged 60–80 $\mu g\ P \cdot L^{-1}$, and phytoplankton was often nitrogen limited. Since 1978 when point-source phosphorus loadings were decreased by about 50%, the phosphorus budgets for the upper Bay of Quinte have become dominated by internal recycling, and total phosphorus concentrations have declined about 35%. As phosphorus loading decreased, phytoplankton biomass and gross primary production rates became phosphorus limited and also declined. The phytoplankton community continued to be dominated by species of *Stephanodiscus* and *Melosira* in spring and summer, respectively, with secondary domination by *Aphanizomenon* and *Anabaena* species (nitrogen-fixing blue-green algae) in late summer. The macrozooplankton community was dominated by small-bodied cladocerans, and no significant changes in composition and production of these forms were detected when phosphorus loadings were reduced. Some larger forms of zooplankton increased in number following phosphorus control. However, planktivorous fish preferred these species as food, and consequently appeared to exert a greater control on the zooplankton community than did the reduction in trophic state. An observed decline in the biomass of oligochaetes, sphaeriids, isopods, and chironomids in the Bay of Quinte was related to a decline in the productivity of the bay resulting from reductions in phosphorus loading. However, another benthic organism, the amphipod *Pontoporeia hoyi*, declined in the mid-1970s and recovered in the lower bay after 1977 when the white perch (*Morone americana*) population collapsed. Shifts in the abundance of many bottom fauna species were greatest in the upper Bay of Quinte and were the reverse of those often observed with deteriorating water quality. Numbers of abundant fish species in the Bay of Quinte, such as alewife (*Alosa pseudoharengus*), white perch, yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum vitreum*), were altered more by climate and predator–prey interactions than by changed nutrient levels. A model of the white perch population indicated that commercial fishing, coupled eventually with a climate-related mortality, reduced the population to a point where predation now appears to control it. Predation on alewife, white perch, and yellow perch by increasing numbers of walleye appears to be controlling the production and biomass of these prey. Increased growth rates of white perch and yellow perch resulting from their lowered abundance have resulted in a higher proportion of their populations becoming large and piscivorous. Models were developed to describe mass water movements in the lower bay, the role of changes in hydrology and sedimentation rates on nutrient budgets, the rate of dissolved oxygen depletion in the deeper, lower bay, and the mass balances of the water column and surface sediment phosphorus pools. Meaningful scientific appraisal of the changes which may continue to occur in the Bay of Quinte depends on regular assessment of several abiotic and biotic parameters. The necessity of maintaining the summer average total phosphorus concentrations below 50 $\mu g \cdot L^{-1}$ to permit continued rehabilitation is emphasized. The critical effects of predator–prey interactions at the secondary and tertiary levels in molding the bay ecosystem were examined. It was concluded that these interactions exert a significant influence on rehabilitation and must be examined in situations where phosphorus controls have been implemented.

Résumé

Minns, C. K., D. A. Hurley, and K. H. Nicholls [ed.] 1986. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

La baie de Quinte du lac Ontario est une importante masse d'eau (254 km^2) qui a divers usages importants pour l'homme, servant notamment à l'approvisionnement en eau pour la consommation et l'industrie, à l'élimination des eaux usées, à la natation, à la navigation, à la pêche à la ligne ainsi qu'à la pêche commerciale. Des scientifiques d'organismes gouvernementaux fédéraux et provinciaux et de certaines universités de l'Ontario ont uni leurs efforts entre 1972 et 1985 afin d'étudier les effets, en 1978, d'importantes réductions de phosphore provenant d'usines de traitement des eaux usées sur les éléments biotiques et abiotiques de la baie. Depuis le début des années 1800, le défrichement des terres a modifié les conditions naturelles dans la baie en augmentant les charges de phosphore, ce qui a eu éventuellement des effets apparents sur certains biotopes. En raison d'une augmentation de la population et de l'usage répandu de détergents ayant une teneur élevée en phosphore, les rejets de phosphore ont monté en flèche après 1940. La qualité de l'eau s'est détériorée au cours des années 50 et 60 affectant sérieusement les approvisionnements en eau des municipalités, les possibilités de loisir ainsi que la pêche sportive et commerciale. L'augmentation de la quantité de phytoplancton a provoqué une pénétration moins grande de la lumière qui, à son tour, a provoqué une réduction de l'abondance de macrophytes submergés après les années 50. Vers les années 70, ces plantes étaient limitées à la zone euphotique peu profonde située à moins de 2 m dans la partie supérieure de la baie et de 4 m dans la partie inférieure. À la fin des années 60 et au début des années 70, le taux de production et la biomasse du phytoplancton et du zooplancton étaient parmi les plus élevés enregistrés dans les eaux douces naturelles. Dans la partie la plus eutrophique de la baie, les concentrations de phosphore total étaient en moyenne de 60 à 80 $\mu \cdot L^{-1}$ de P et le phytoplancton était souvent limité par l'azote. Depuis 1978, année où les charges ponctuelles de phosphore ont diminué d'environ 50 %, les bilans de phosphore dans la partie supérieure de la baie de Quinte ont été dominés par une recyclage interne et les concentrations de phosphore total ont diminué d'environ 35 %. Au fur et à mesure que la charge de phosphore diminuait, la biomasse du phytoplancton et la production primaire brute sont devenues limitées par le phosphore et ont également baissé. La communauté phytoplanctonique a continué d'être dominée par des espèces de *Stephanodiscus* et de *Melosira* respectivement au printemps et en été, suivi en deuxième place par des espèces d'*Aphanizomenon* et d'*Anabaena* (algue bleu-vert fixatrice d'azote) à la fin de l'été. La communauté de zooplancton macroscopique a été dominée par de petits cladocères et on n'a décelé aucun changement important dans la composition et dans la production de ces formes lorsque les charges de phosphore étaient réduites. Certaines formes plus grosses de zooplancton ont augmenté en nombre à la suite de la réduction du phosphore. Cependant, les poissons planctonivores ont préféré ces espèces comme source de nourriture et ont semblé par conséquent exercer un plus grand contrôle sur la communauté zooplanctonique que ne l'a fait la diminution du niveau trophique. On a relié une diminution observée de la biomasse des oligochètes, des sphaeriidés, des isopodes et des chironomidés dans la baie de Quinte à une diminution de la productivité de la baie découlant de la réduction des apports de phosphore. Cependant, un autre organisme benthique, l'amphipode *Pontoporeia hoyi*, a connu une baisse au milieu des années 70 et s'est rétabli dans la partie inférieure de la baie après 1977, lorsque la population de barets (*Morone americana*) s'est affaissée. Les changements dans l'abondance d'un grand nombre d'espèces fauniques benthiques ont été les plus grands dans la partie supérieure de la baie de Quinte et ont été à l'opposé de ceux qu'on observe souvent lorsque la qualité de l'eau se détériore. Le climat et les interactions prédateur/proie ont influé davantage sur la population des espèces de poisson abondantes dans la baie de Quinte, comme le gaspareau (*Alosa pseudoharengus*), le baret, la perchaude (*Perca flavescens*) et le doré jaune (*Stizostedion vitreum vitreum*) que les changements dans la concentration des substances nutritives. Un modèle de la population de barets a montré que la pêche commerciale, associée éventuellement à une mortalité liée au climat, a réduit la population à un point tel que la prédation semble maintenant la contrôler. La prédation exercée sur les gaspareaux, les barets et les perchaudes par un nombre accru de dorés semble contrôler la production et la biomasse de ces proies. Le rythme de croissance accru des barets et des perchaudes découlant de leur plus faible abondance a fait qu'une plus forte partie de leurs populations est devenue grosse et piscivore. On a élaboré des modèles pour décrire le déplacement des masses d'eau dans la partie inférieure de la baie, le rôle des changements dans l'hydrologie et les taux de sédimentation sur les bilans des substances nutritives, le taux de diminution d'oxygène dissous dans la partie inférieure et plus profonde de la baie et l'équilibre de masse de la colonne d'eau et des réservoirs de phosphore dans les sédiments de surface. L'évaluation scientifique valable des changements qui peuvent se poursuivre dans la baie de Quinte dépend de l'évaluation régulière de plusieurs paramètres biotiques et abiotiques. On met l'accent sur la nécessité de maintenir les concentrations moyennes de phosphore total pendant l'été en-dessous de 50 $\mu g \cdot L^{-1}$ pour que le rétablissement se poursuive. On a étudié les effets critiques des interactions prédateur/proie aux niveaux secondaire et tertiaire pour modeler l'écosystème de la baie. On conclut que ces interactions ont une influence importante sur la remise en état des populations et doivent être examinées dans les cas où on a mis en oeuvre des mesures de réduction du phosphore.

Overview of Project Quinte — 1972–82

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Background information is given on the initiation of a multi-agency research project to compare limnological features of the Bay of Quinte, Lake Ontario, before and after reduction in phosphorus inputs. Water quality trends and changes in fisheries are summarized. The experimental management approach and ecological framework for this research are discussed in general terms. A total of 23 reports on chemical and physical limnology, phytoplankton, macrophytes, zooplankton, benthos, and fish accompany this introductory report.

On présente des renseignements de base sur la création d'un projet de recherches regroupant plusieurs organismes et destiné à comparer les caractères limnologiques de la baie de Quinte (lac Ontario) avant et après la réduction des apports de phosphore. On résume les tendances observées dans la qualité de l'eau et les changements survenus en ce qui a trait aux pêches. On discute en termes généraux de la méthode de gestion expérimentale adoptée et du cadre écologique de cette recherche. Vingt-trois rapports portant sur la limnologie chimique et physique, le phytoplancton, les macrophytes, le zooplancton, le benthos et les poissons accompagnent ce rapport préliminaire.

Introduction

The purpose of this introductory paper is to describe the Bay of Quinte in general terms, to review the history of water quality and fisheries in the bay and the principal management initiatives, to explore further the scientific rationale and approaches which tied together the participants in Project Quinte, and to assess some of the accomplishments.

In the mid-1960's public outcry and government attention were focussed on the problem of excessive nutrient enrichment of the waters of the lower Great Lakes. By 1970 the term "eutrophication" was in everyday use and the campaign to reduce P loadings began in earnest with regulated decreases in P content in detergents. In 1970 the International Joint Commission (IJC) recommended "further reduction, as a matter of urgency, of the remaining phosphorus in municipal and industrial waste effluent discharging to Lake Erie, Lake Ontario and their tributaries and to the International Section of the St. Lawrence River, with a view to achieving at least an 80 percent reduction by 1975 and thereafter additional reduction to the maximum extent possible by economically feasible processes" (IJC 1970). By 1972 the commitment of governments was formalized in the Canada–U.S. Great Lakes Water Quality Agreement, and a 5-yr program was initiated to reduce industrial and municipal inputs of P and to investigate further the significance of non-point sources. The Agreement was renewed in 1978 and called for a broader approach to P control to meet specified target loadings.

In 1972 there were no case histories that showed water quality improvements achieved by selective point-source P reductions. Arguments for P removal (and sometimes against) were based on laboratory experiments (Vallentyne et al. 1970), additions, but not reductions, of P to small lakes (Johnson and Vallentyne 1971), diversions of municipal wastes, as in the case of Lake Washington (Edmondson 1972), and the empirical relationship between P loadings to lakes and their apparent trophic state (Vollenweider 1968).

The decrease in numbers of large piscivores in the Bay of Quinte occurred during the years of increasing eutrophy, and was circumstantially linked with eutrophication (Hurley and Christie 1977). Other factors, such as excess fish harvest and the proliferation of exotic species, also destabilized the fish community of the bay (Christie 1972). The combined effect was the proliferation of small, relatively shortlived benthivorous and planktivorous species such as alewife (*Alosa pseudoharengus*) and white perch (*Morone americana*). The impact of these species on benthic fauna and herbivorous zooplankton may have been sufficient to permit dense blooms of algae to form in response to accelerating point-source P loadings, and thereby produce the resultant drop in water transparency (Andersson et al. 1978; Shapiro 1980), occasional oxygen depletion, and general deterioration of water quality.

The improvement in habitat resulting from P reductions was intuitively believed to benefit the fish community of the bay, although likely mechanisms were not well understood. Would reduction in P relieve this destabilizing influence sufficiently to permit the system to proceed along its successional path to a more mature and stable system (Odum 1969)? Or, would persistence of large numbers of small planktivores continue to crop herbivorus zooplankton sufficiently that algal density would remain high in spite of nutrient reduction (Shapiro 1980)? In this latter case, habitat improvement would require manipulation of fish stocks, probably by introduction of piscivores and harvest of planktivores. In any event, the study would require many years of effort to permit enough generations of fish to pass through the system to assess the response adequately.

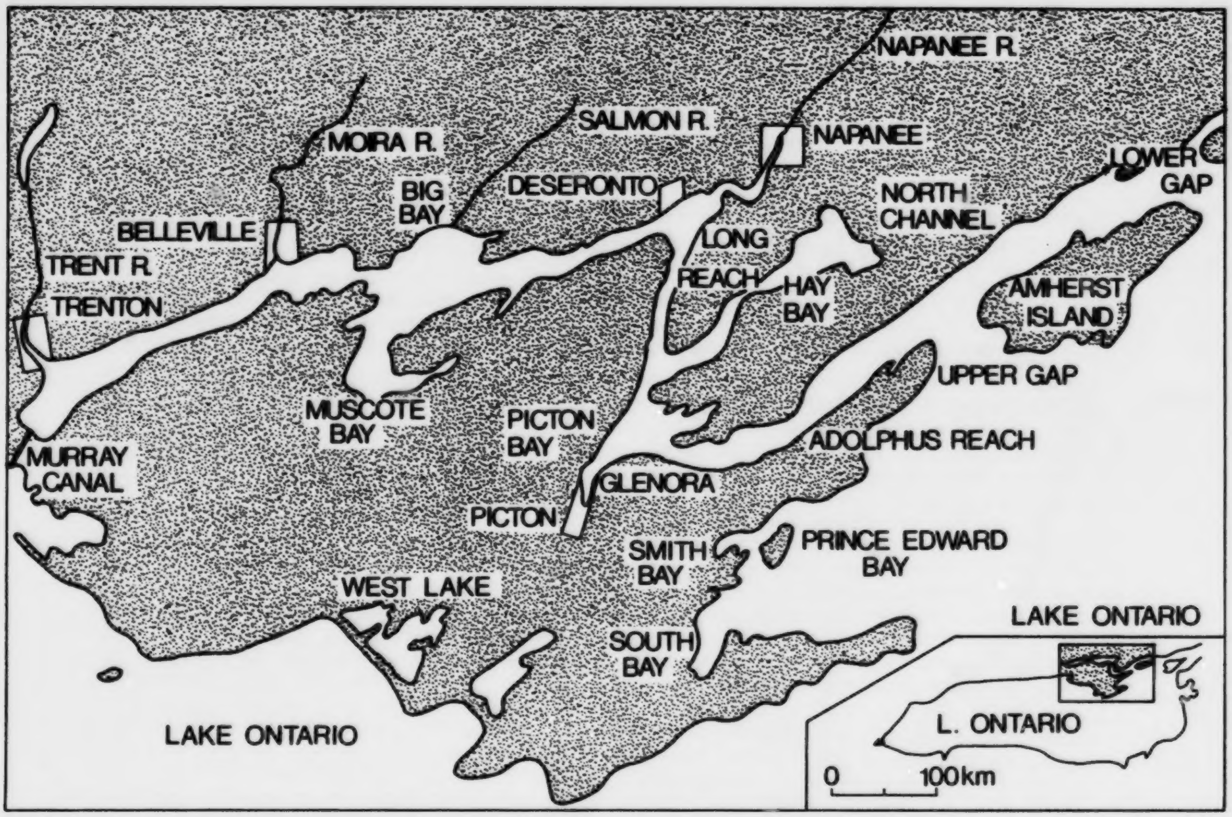

FIG. 1. Location of the Bay of Quinte in eastern Lake Ontario. Main rivers, urban areas, and principal bays and reaches are shown.

The presense of useful background data made the heavily enriched Bay of Quinte an attractive and much needed potential case history for fisheries scientists and water-quality managers. The attraction of the Bay of Quinte to limnologists was the simplified logistics and economy of working in a smaller basin and the opportunity to collaborate with fisheries scientists. Participants in Project Quinte shared the concern that at least several years of uninterrupted study were necessary to build on existing background studies. Furthermore, relevance of studies on the Bay of Quinte to management of other Great Lakes waters was obvious. There was a close resemblance between aquatic communities and limnology of the Bay of Quinte, from upper to lower bay, and Lake Erie, from west to east. Prior to P removal, annual P loading rates in the Bay of Quinte and Lake Erie were high, 1.47 g/m^2 in the former and 1.07 g/m^2 in the latter (Johnson and Owen 1971). In both areas, poorest water quality occurred where effective loading rates were much greater than these averages. Insights obtained from either one of these heavily stressed areas might be applicable to the other, and indeed to any area where excessive nutrient enrichment was a destabilizing influence.

In this context, in 1972 several limnologists and fisheries scientists from the Ontario Ministry of Natural Resources, Ontario Ministry of the Environment, Fisheries and Marine Service of the Canada Department of Environment, University of Guelph, and Queen's University initiated a multi-year study of the response of the Bay of Quinte to the P-reduction program. This *Special Publication* contains accounts of much work done by the Project Quinte group through the period 1972–82.

The Bay of Quinte Ecosystem

The Bay of Quinte is a Z-shaped bay, 64 km long and 254 km in area, on the northeastern shore of Lake Ontario (Fig. 1). The upper bay, 35 km long, consists of several connected basins approximately 4–8 m deep. The greatest development in extent and rate of human population growth is along the north shore of the upper bay, where the total population in 1982 was about 60 000. The watershed of the Bay of Quinte, totaling 18 200 km^2, consists of about one-half Precambrian Shield in the north and one-half Paleozoic limestones in the south. The limestone plain has little overburden in many areas, although extensive sand and clay plains occur adjacent to the bay. The major rivers enter along the north shore: the Trent River draining 12 600 km^2, the Moira River draining 2 700 km^2, and the Salmon and Napanee rivers together draining 1 660 km^2. The middle bay is 13 km long, only about 0.8 km wide at the north end, and 5.6 km wide near Picton, and increases from 6 to 17 m in depth from north to south. The lower bay is 16 km long, about 3 km wide, and the maximum depth increases from 17 to 52 m toward the bay mouth. The watershed of the middle and lower bays is not extensive, but includes Hay Bay, 11 km long, and its watershed. Only about 15 000 people reside in the towns and townships bordering the middle and lower bays.

Two passages, one at each end of Amherst Island, join the lower bay and Lake Ontario. The western passage, the Upper Gap, is 2.4 km wide and 13 m deep, and the eastern passage, the Lower Gap, is of similar width but twice as deep. The upper arm of the bay is connected westward to Lake Ontario for navigation by the Murray Canal, which is only 23 m wide and 3 m deep.

Trenton, Belleville, Deseronto, Napanee, Picton, and two bases of the Canada Department of National Defence (DND) near Trenton and Picton (the latter was closed in 1969) discharge treated wastewaters to the bay. These had conventional secondary or partial waste treatment until 1975 (DND Trenton), 1976 (Belleville, Trenton, Deseronto, and Picton), and 1977 (Napanee), when P removal to a target level of 1.0 mg/L residual was implemented. P content in laundry detergents had already been reduced to 20% (P_2O_5) in 1970, and further reduced to 5% (P_2O_5) on January 1, 1973, by federal regulations under the Canada Water Act. By 1979 further P reductions, to 0.5 mg/L in final effluent, were required at all treatment plants during the May–October period, but total compliance with this requirement has not been achieved over all months. A high flushing rate favoured good results from additional point-source P control during the summer months, after large springtime P inputs were flushed from the system. The bay flushing rate is approximately 10 times per year, and the flushing time during March and April is about 1 mo.

Two municipalities, Belleville and Deseronto, take water from the bay for domestic and industrial use. For many years, water quality was often unsatisfactory and treatment to produce potable water was beset with difficulties attributable to the long periods of high algal density and thick blooms of blue-green algae that developed over several weeks of warm weather each year. In the early 1970's a proposal for a water-supply pipeline from Lake Ontario to the Belleville–Trenton area was indefinitely postponed while the P-control program was implemented and evaluated. The bay is used throughout its length for varied recreational activities, many of which have been curtailed by unsatisfactory water quality.

Water Quality Trends

The natural trophic state of the lower Bay of Quinte prior to the late 1800's, determined from chemical and biological features of sediment cores, was slightly to moderately oligotrophic (Warwick 1980). A period of low productivity, 1840–60, coincided with increased sediment load following land clearing. The eutrophic state was evident in cores from 1890–95 and accelerated to a hypereutrophic state in the 1950's.

Deterioration in water quality has been observed since about 1930. Early records at the Belleville and Picton water-supply plants showed that blooms of blue-green and green algae were troublesome because they clogged filters, especially in August and September. The filters in the Belleville plant required more frequent backwashing after 1934. McCombie (1967) reported that concentrations of algae in the upper bay were about 10 times those in the middle bay, and 100 times those near the mouth. Although there was no definite evidence of an increase in algae at the bay mouth since 1945 when Tucker (1948) carried out his investigation, diatoms were relatively less abundant and blooms of the blue-green alga *Aphanizomenon* began 1 mo earlier in 1963 and 1964 than in 1945. Secchi disc readings of less than 0.3 m accompanied the blue-green algal blooms in the upper and middle bays in the 1960's (Johnson and Owen 1971). Occasional extinction of dissolved oxygen was found by McCombie (1967) in subsurface waters near Belleville under calm conditions in summer, and later in the middle bay near the confluence of Hay Bay by D.A. Hurley (pers. comm.) In Adolphus Reach, oxygen was depleted to low levels (1–2 mg/L) in late summer in hypolimnetic waters. Macrophytes, which had been common and rich in species diversity over an extended period, became locally abundant in the early 1960's to the point that control was necessary in some locations in the upper bay. Subsequently, macrophytes declined when algal standing stocks increased (Crowder and Bristow 1986).

The diverse habitat of the Bay of Quinte currently supports at least 62 species of fish from 44 genera (Hurley 1986). Most represent a warmwater association, but several cold-water forms enter the bay from Lake Ontario at some time in the year. In the past, the bay supported significant commercial fisheries for lake whitefish (*Coregonus clupeaformis*) and lake herring (*Coregonus artedii*), plus both commercial and sport fisheries for walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) (Christie 1973). In the early 1970's the commercial fishery was restricted largely to carp (*Cyprinus carpio*), American eel (*Anguilla rostrata*), white perch, and yellow perch, while sport fishing had virtually disappeared in the bay.

In the years 1972–77 the fish population was dominated by alewife and white perch, with lesser numbers of yellow perch, rainbow smelt (*Osmerus mordax*), brown bullhead (*Ictalurus nebulosus*), and trout-perch (*Percopsis omiscomaycus*). It is postulated that the near absence of large piscivores in this period facilitated the proliferation of prey species such as alewife and white perch (Minns and Hurley 1986).

A massive die-off of white perch occurred overwinter in 1977–78, and large year-classes of both walleye and yellow perch developed in the following spring. Consequently the fish community in the bay shifted to one that was controlled by piscivores. Growth rates among the remaining white perch increased significantly (Minns and Hurley 1986) and abundance of alewife declined dramatically (Hurley 1986).

The Quinte Experiment

Although there has been considerable discussion of the "ecosystem approach" in resources management in the Great Lakes (IJC 1978), inadequate attention has been focused on infrastructure and methodologies useful in implementation of this policy principle. Recent initiatives in strategic planning by fisheries agencies have advocated "experimental management" (Loftus et al. 1978). Experimental management could be broadly defined in terms of water resources, or natural resources generally, with the same intention of learning by managing through hypotheses-testing experiments in the real world.

The P-management strategy in the Great Lakes has followed this iterative course with alternating reference studies and management agreements over the past 20 yr. In the context of Project Quinte, experimental management has been an important platform for management because it encourages the intensity of effort needed to address complex ecological problems, allows mid-course adjustments by timely transfer of information, and correction of deficiencies in knowledge. For researchers, the approach offers the opportunity to single out effects of specific stress factors and to influence management without foregoing the opportunity to pursue broad questions that require understanding of the whole system. Economies and significant improvement in public support consequently should accrue to both management and research.

The Bay of Quinte is particularly suited to the experimental management approach. First, it is an important and representative subsystem of the lower Great Lakes, yet to a large extent it is discrete. It is also small enough to permit intensive study on moderate budgets sustained over several years. There is a significant amount of baseline data. There is a group of regional managers and scientists with appropriate experience, interest, and concern. Working together, these managers and scientists have developed the objectives for nutrient control and fisheries management within an experimental framework. They have met annually from the outset to review research findings and to discuss management implications. The scientists have produced annual reports, but have been criticized for publishing little else. There appeared, however, to be little need for rapid publication of the results because of the continual contact between scientists and managers, the expectation of stronger data series with each new year's work, and the desire to follow the experiment through the recovery phase. At the local management level, the close contact between managers and scientists in the experimental management of the bay obviated the need to communicate through the primary literature. Later publication would allow a more comprehensive account of the experiment, which would be more useful both to research and management elsewhere.

In 1972, at the outset of Project Quinte, the common objective of researchers and managers was straightforward: would P reduction to prescribed levels at point sources increase production of economically important fish stocks, and improve water quality both for municipal supplies and for various recreational activities in the Bay of Quinte in a reasonable length of time? Prior to implementation of P control, only 20–40% of the P loading was attributable to municipal inputs, and 60–80% entered via rivers. Some water-quality managers were doubtful that P reduction in point sources would be effective because these were a low proportion of total P inputs. Johnson and Owen (1971) argued that low-volume, high-concentration point sources, such as those in the Bay of Quinte, have a greater impact on water quality during the growing season than high-volume, low-concentration inputs from rivers. They recommended point-source P control to reduce ambient P concentrations and algal stocks. However, even with P control, improvement in water quality might be delayed by shallow, nutrient-enriched sediments in the entire upper bay, which are subject to periodic resuspension (although P sediment–water interactions in shallow systems are not well understood).

Search for an Ecological Framework

The attempt to develop a scientific framework for experimental management of the bay is ongoing. Discussion of the ecological framework focused on the interactions among water, sediment, macrophytes, and phytoplankton in determining successional stages in eutrophication and rehabilitation of the bay. The questions of most general interest to researchers and managers concerned the speed with which eutrophic and hypereutrophic states might be reversed by control of P input, and whether animal communities would shift from their hypereutrophic state back to eutrophic or mesotrophic counterparts.

The relationship between external P loading and internal fluxes, especially where their relationship affects phytoplankton blooms, has been of considerable interest. Internal sources include not only resuspended sediments, but also hypolimnetic waters of the lower bay which become mixed by upwelling into surface waters of the middle bay. One external P source, now better understood because of the study, is the intrusion of Lake Ontario water into the lower and middle bays. Also, short-term oxygen depletion in the upper bay during periods of calm weather and seasonal depletion in the lower bay were expected to influence P dynamics.

Rates of production of zooplankton, benthic macroinvertebrates, and fish and efficiencies of use of energy in relation to quantity and quality of food resources were to be examined in the context of changes in P loading and trophic state. Although these changes have been gradual and are probably incomplete to date, most comparisons have been made between periods before P control (prior to 1977) and afterwards (1977–82). Inferences about communities dominated by macrophytes were facilitated by comparisons with nearby waters, especially West Lake, Prince Edward Bay, and inner Hay Bay. Structure of aquatic communities was examined in terms of habitat diversity as influenced by macrophytes, substrate, turbidity, and oxygen conditions, again in a pre- and post-P-control context. We tried to avoid the common tendency to view intertrophic level relationships in one-way cause-effect systems (plants–invertebrates–fish as secondary consumers; fish as tertiary consumers).

Long-term studies confront researchers with variability due to fluctuations in natural factors (solar radiation, winds, precipitation, currents, temperature), which confound trends attributable to management initiatives. P-mangement initiatives and predicted responses usually are based on "average conditions." However, an understanding of system responses to natural factors is necessary in order to evaluate programs, to fine tune measures, and possibly to redefine requirements based to some degree on extremes (as in flood protection for example). Natural annual and seasonal variations in structure, production, and abundance at all trophic levels, and possible compensating mechanisms leading to "natural limits" on variations, were of considerable interest. Individual views were held for both strong homeostatis and highly stochastic behaviour.

The overall ecological framework for the Quinte study was not designed at the outset. The merits and faults of various approaches were debated through the course of the study. Despite generally successful use of several deterministic and empirical models and availability of a broad and long data series, much of which dealt with dynamic properties, there was little enthusiasm for developing a detailed trophodynamic simulation model of bay limnology. Perhaps the Project Quinte group understood bay limnology sufficiently to appreciate how much it did not know. Certainly the group was apprehensive about the number of weakly supported assumptions that would have been required. The practical alternative to a detailed simulation was to accentuate the key features of ecosystem change in a model of trophic succession, that is, to focus on the transition from known states to structurally and functionally different states, which may be based on different threshold P loadings. The emphasis was on homeostatic properties of these successional states, contributions by principal plant and animal assemblages to the self-perpetuation of these states, and the shift from one state to another by catastrophic events as, for example, the reduction of macrophytes by phytoplankton blooms and the temperature-induced mortality of white perch. Effects of variations in natural factors probably are damped more often than changes attributable to man, as, for example, greater P loadings in runoff are usually accompanied by greater flows and greater flushing. High P loadings from pollution sources are undiluted and therefore more likely to trigger change. Resiliency in communities, although known to be partly the property of each species, probably is related also to differences in effect between natural and man-made stress of the same type, but different character. The approach would place emphasis on critical limnological events, such as oxygen depletion over sediments, submarginal light regimes for macrophytes, and critical stages in life histories of species relative to competitors in these community and ecosystem states. The approach appeared to be in harmony with the amount and type of data available. It seemed useful to managers, it maintained a sound, albeit simple, ecological basis for the study, and, possibly most important, the group felt confident in pursuing such an approach at that time. The potential of this ecological framework has been realized only partially at this stage, but it remains as a goal, for the sake of continuity, to guide future work.

Overview of Accomplishments

A strong foundation is in place for designing optimum water-quality management programs, which may consider effects of P loadings from different sources, flushing rates, variability in climate, and expected responses. For example, impacts of point-source and non-point P control measures may be compared. Future stresses on the Quinte system, from increased P loadings, inflow manipulation, or possible expansion of macrophytes, may be examined in the light of present findings.

There are several practical accomplishments that have permitted a project of this size to continue in such an informal organizational framework. Perhaps the most significant has been an optimum level of administrative direction to the project. The primary questions asked were posed by scientists, with the view to answering them from both a scientific and a management-orientated viewpoint. Managers and scientists interacted at annual meetings where progress was discussed; an extensive annual report was prepared each year and circulated to senior management. This "mutual accountability" reinforced our view that ecological questions and practical management questions are much the same. Scientists involved in Project Quinte have appreciated the opportunity to intereact with managers and to influence management without being overmanaged by a plethora of steering committees, reviews, and reorganizations.

In order to answer scientific and management questions, several years of research are necessary because variations in climate and the biota are unpredictable and may mask the effects of the so-called controlled variable. Furthermore, these random influences should be adequately understood and become part of the management rationale. One of the main values of the Quinte study probably is in showing the magnitude of natural variations relative to changes attributable to management, and, hopefully in the future, incorporating natural stochastic factors in the nutrient-control strategy. In addition, this time series was expected to provide an efficient, economical, and meaningful monitoring approach to assess improvements, and an early-warning system if degradation occurs in future years. Studies are continuing at the present time. Longer-term studies on selected representative systems, with carefully controlled management initiatives, are fundamental to the "experimental management" approach. Project Quinte is a useful pilot project which embodies this philosophy.

In terms of scientific achievements, we feel we have posed many appropriate questions and answered a few. These are reported in the papers that follow. Multi-year studies breed considerable caution in investigators, and rightly so, because the answers to many questions become more elusive as the random elements of nature are revealed. At this point we have good descriptive information on the Bay of Quinte, a fair understanding of dynamics, and only minimal knowledge of mechanisms. However, as the database grows, more and more hypotheses will become testable. Controlled experiments in field and laboratory should become increasingly important in testing hypotheses on mechanisms.

Acknowledgments

We wish to express our appreciation of the efforts of our colleagues who contributed to this special compilation of articles from the *Canadian Journal of Fisheries and Aquatic Sciences*. These researchers maintained a dedicated interest over the years, not only to the Bay of Quinte as an important resource, but also to the rationale of interagency cooperation in experimental management, which always appeared to be so worthwhile in the complex environment in which we have tried to work effectively. All of us owe special thanks to the many summer students and technicians who performed their work in exemplary ways, including Bud Timmins, Wayne Hyatt, Gary Koteles, Steve Smith, Barry Moore, Kevin Young, Michael Jackson, Kevin Roslyn, Kevin Loftus, Kent Wylie, Colin Baile, Gordon Lambert, Roger Sundre, and Kevin Richardson of CCIW and Ken Scott, Steve Leonard, Ron McIntosh, and Cecil Lobb of the Glenora Fisheries Research Station. Coxswains and crew members of federal and provincial vessels were consistently cooperative and helpful far beyond the requirements of their jobs. Over the past dozen years we received tangible support and considerable encouragement from Jack Christie, Ken Loftus, Andy Lawrie, and Eric Gage of the Ontario Ministry of Natural Resources, and Ken Lucas, at that time head of the federal Fisheries and Marine Service.

References

ANDERSSON, G., H. BERGGREN, G. CRONBERG, AND C. GELIN. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9–15.

CHRISTIE, W. J. 1972. Lake Ontario: effects of exploitation, introductions and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

1973. A review of the changes in fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23:65 p.

CROWDER, A., AND M. BRISTOW. 1986. Aquatic macrophytes in the Bay of Quinte, 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

EDMONDSON, W. T. 1972. Nutrients and phytoplankton in Lake Washington, p. 172–193. *In* Nutrients and Eutrophication, Special Synopsia Vol. 1. American Society of Limnology and Oceanography, Inc., Grafton, WI.

HURLEY, D. A. 1986. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

HURLEY, D. A., AND W. J. CHRISTIE. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish Res. Board Can. 34: 1849–1860.

INTERNATIONAL JOINT COMMISSION (IJC). 1970. Pollution of Lake Erie, Lake Ontario and the international section of the St. Lawrence River. IJC, Ottawa, Ont. 105 p.

1978. The ecosystem approach: scope and implications of an ecosystem approach to transboundary problems in the Great Lakes Basin. Great Lakes Research Advisory Board, IJC, Windsor, Ont. 47 p.

JOHNSON, M. G., AND G. E. OWEN. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

JOHNSON, W. E., AND J. R. VALLENTYNE. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. J. Fish Res. Board Can. 28: 123–128.

LOFTUS, K. H., M. G. JOHNSON, AND H. A. REGIER. 1978. Federal–provincial strategic planning for Ontario fisheries: management strategy for the 1980s. J. Fish. Res. Board Can. 35: 916–927.

MCCOMBIE, A. M. 1967. A recent study of the phytoplankton of the Bay of Quinte 1963–1964. Proc. 10th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.: 37–62.

MINNS, K. C., AND D. A. HURLEY. 1986. Population dynamics and production of white perch, *Morone americana*, in the Bay of Quinte, Lake Ontario, p. 215–223. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

ODUM, E. P. 1969. The strategy of ecosystem development. Science (Wash., DC) 164: 262–270.

SHAPIRO, J. 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes, p. 105–116. *In* J. Barica and L. R. Mur [ed.] Developments in hydrobiology. Vol. 2. Dr. W. Junk bv Publishers, The Hague, Boston, and London.

TUCKER, A. 1948. The phytoplankton of the Bay of Quinte. Trans. Am. Microsc. Soc. 67: 365–383.

VALLENTYNE, J. R., W. E. JOHNSON, AND A. J. HARRIS. 1970. Visual demonstration of the beneficial effects of sewage treatment of phosphate removal on particulate matter production in waters of Lake Erie and Lake Ontario. J. Fish. Board Can. 27: 1493–1496.

VOLLENWEIDER, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD, Paris, France.

WARWICK, W.F. 1980. Palaeolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 117 p.

Review of Postglacial Environmental Changes and Cultural Impacts in the Bay of Quinte

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Sly, P. G. 1986. Review of postglacial environmental changes and cultural impacts in the Bay of Quinte, p. 7–26. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control land ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Rising waters began to inundate the Bay 9000–10 000 B.P. and overtopping of the Telegraph Narrows sill took place 2000–3000 yr ago. The natural trophic state was significantly influenced by climate. Lower Bay waters changed from slightly oligotrophic to moderately oligotrophic, probably in response to hemispheric cooling between 1500–1000 B.P., and changes in trophic state appear to respond more to temperature than to long-term water level fluctuations. Trends in the erosion index particle-size data from the Glenora core are largely comparable with recent Lake Michigan water level changes. Cultural impacts, since the early 1800's, have overriden natural conditions in the Bay. Increased loadings of total P were first derived from soil loss at the time of land clearance, and later from municipal treatment plants, detergents, and fertilizers. Parts of the Bay became strongly eutrophic by the mid-1950's, but water quality has improved since plant upgrading in 1978. Heavy metals enrichment, especially As from mining in the Moira watershed, occurred after the 1850's; pesticides were introduced 35–40 yr ago and some sources continue to release other persistent contaminants into the Bay.

Les eaux montantes ont commencé à inonder la baie de 9 000 à 10 000 ans avant notre ère et le goulet Telegraph était encore submergé il y a 2 000 à 3 000 ans. Le climat a grandement influé sur la condition trophique naturelle. Les eaux de la partie inférieure de la baie, qui étaient légèrement oligotrophes, sont devenues modérément oligotrophes, probablement à la suite du refroidissement de l'hémisphère nord, entre 1 500 et 1 000 ans avant notre ère, et les modifications de la condition trophique semblent être liées davantage à la température qu'aux variations à long terme du niveau de l'eau. Les tendances observées dans les données sur la taille des particules en ce qui concerne l'indice d'érosion tirées de la carotte prélevée à Glenora sont dans une large mesure comparables aux changements récents du niveau de l'eau dans le lac Michigan. Depuis le début des années 1800, le développement de la civilisation a modifié les conditions naturelles dans la baie. Il y a eu des charges accrues de P total provenant d'abord de la perte de sol au moment du défrichement des terres puis, par la suite, des usines de traitement des eaux domestiques, des détersifs et des fertilisants. Des parties de la baie sont devenues très eutrophes vers le milieu des années 1950, mais la qualité de l'eau s'est améliorée après la modernisation des usines en 1978. La concentration des métaux lourds, principalement de l'As provenant de l'exploitation minière, a augmenté après les années 1850; les pesticides ont fait leur apparition il y a 35 à 40 ans et certaines sources continuent à déverser d'autres contaminants permanents dans la baie.

Introduction

This contribution provides historical and geographical perspectives which form a background for the other papers that deal with more specific limnological and cultural impact studies in this Project Quinte series: geological and climatological changes are described and the development of settlement and agricultural, industrial activities, and population shifts are traced, with emphasis on the past 200 yr. Supporting evidence from available sediment cores has been reevaluated and is presented as a means of summarizing the more recent changes and events within the Bay.

Historical information is presented in detail as a single source of reference for use with this and other papers of this series. The significance of various forms of impact in the Quinte area are summarized at the end of each section.

General Setting

Physiography

The Bay of Quinte lies on the north shore of Lake Ontario but is largely separated from the main lake by a barrier, formed by Prince Edward County and Amherst Island. The Bay has a complex shape, and the direct distance between Trenton and Kingston is about 90 km. Water depth generally increases from west to east: 1–3 m near Trenton, 5 m over much of Big Bay, 7 m in the Long Reach near Napanee, 14 m in Picton Bay, and more than 60 m in the North Channel opposite Amherst Island (Fig. 1). The outlet of the Bay into the Kingston or eastern basin of Lake Ontario is controlled by sill-like features having maximum depths of more than 25 m at the Upper and Lower Gaps near Amherst Island. The maximum width of the Bay is about 3.5 km and there are major points of constriction at Belleville, Telegraph Narrows, Ram Island, and Glenora.

Land is low lying to the north and east of the Bay, except between Napanee and Hay Bay. The Napanee plain between Trenton and Kingston (Chapman and Putnam 1951) is characterized by a generally flat surface of glacially scoured bedrock and bevelled till, locally modified by extensive drumlin fields. South of the Bay, scarp-like features back much of the shore east of Belleville. Along the Long Reach and Adolphus Reach, the south and west shores rise to about 50 m above lake level, and near Glenora, the elevation locally exceeds 75 m. The low plateau, above the scarp, dips gently southwest towards Lake Ontario.

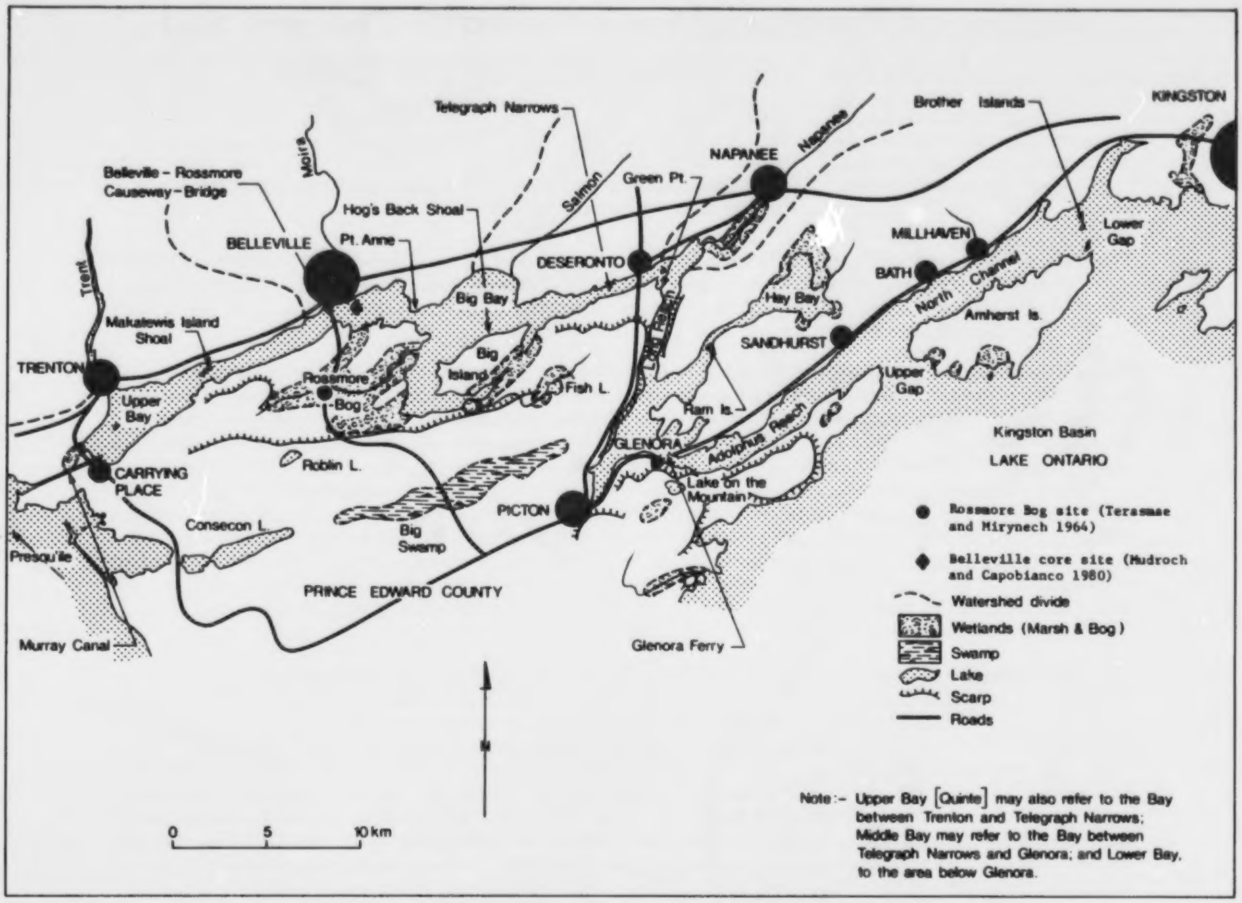

Telegraph Narrows
Brother Islands
KINGSTON
Belleville - Rossmore Causeway - Bridge
Moira
Napanee
NAPANEE
Salmon
Green Pt.
Hog's Back Shoal
BELLEVILLE
Pt. Anne
DESERONTO
MILLHAVEN
Lower Gap
Trent
Big Bay
BATH
North Channel
Hay Bay
Amherst Is.
Makatewis Island Shoal
SANDHURST
Long Reach
Big Island
TRENTON
Rossmore
Bog
Fish L.
Upper Gap
Upper Bay
Ram Is.
Kingston Basin
GLENORA
Adolphus Reach
LAKE ONTARIO
Roblin L.
CARRYING PLACE
Lake on the Mountain
Consecon L.
Big Swamp
PICTON
Presqu'ile
PRINCE EDWARD COUNTY
Murray Canal
Glenora Ferry
N
0
5
10 km
Rossmore Bog site (Terasmae and Mirynech 1964)
Belleville core site (Mudroch and Capobianco 1980)
Watershed divide
Wetlands (Marsh & Bog)
Swamp
Lake
Scarp
Roads
Note :- Upper Bay [Quinte] may also refer to the Bay between Trenton and Telegraph Narrows; Middle Bay may refer to the Bay between Telegraph Narrows and Glenora; and Lower Bay, to the area below Glenora.

FIG. 1. Bay of Quinte, showing reference locations, watershed divides, and physiographic features.

Circulation and Stratification

Circulation in the Bay generally conforms to a west–east flow, although seiching occurs in both directions. During the summer months, the shallow Upper Bay remains well mixed and permanent thermal stratification is absent. In parts of Picton Bay and below Glenora, however, the summer thermocline is well developed and frequently tilted by local wind stress. Stratification influences the exchange of Lower Bay waters with Lake Ontario, and during mid- and late summer, intrusions of cold bottom water have been recorded as far up the Bay as the south end of the Long Reach; these are accompanied by a compensatory outflow of warm surface water. Under calm conditions, during the stratified period, the sediments and bottom waters of parts of the Upper Bay may become temporarily anoxic. At such times, sediment P release is greatly increased, and further accentuates eutrophic conditions in the Bay.

Although flushing of the Bay occurs only 0.25–1.0 times during the May–September period and 2–3 times per year (Minns et al. 1986), temperature profiles across the Middle and Lower Bay during summer stratification indicate that both vertically and horizontally entrained flows occur; thus, on a local basis, there may be significant changes in water quality which are independent of overall water quality in the Bay. Such changes can be further modified by the presence of free surface and internal oscillations. Prinsenberg (1978) reported Bay mode periods of 15.5–35 h and a Lake Ontario period of 5.2 h. The effects of nutrient loadings from external sources to the Bay are most evident during periods of low flow.

Geology

Bedrock

Except for a small inlier of Precambrian rock in northern Prince Edward County (Kay 1942), thin shaley limestones of mid-Ordovician age completely surround the Bay of Quinte. Fine limestones and interbedded grey shales of the Black River Group underly most of the Napanee plain at shallow depth (Liberty 1971), but elsewhere (largely in Prince Edward County) the harder and more nodular limestones of the Trenton Group provide a slightly more resistant capping (Liberty 1961a).

Glacial Evolution

The Bay of Quinte is made up of a series of interlinked and glacially scoured depressions, which reflect a coincidence between the direction of late glacial ice flow and earlier drainage patterns (Starling 1978). The generally northeast–southwest alignment of features follows structural control (particularly jointing), and the narrow and steep-sided section of the Long Reach may follow a north–northeast/south–southwest fault line (Liberty 1961a, 1961b). The unique depressions that form Lake

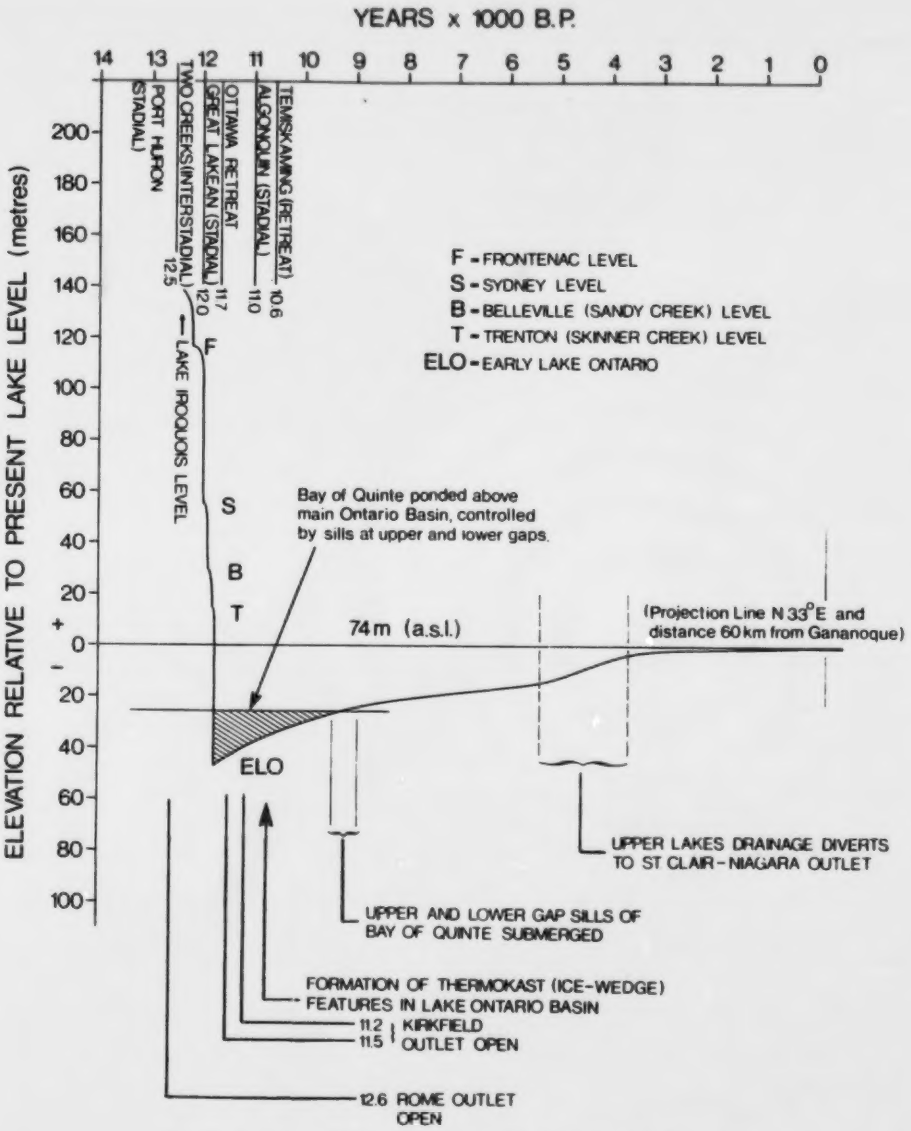


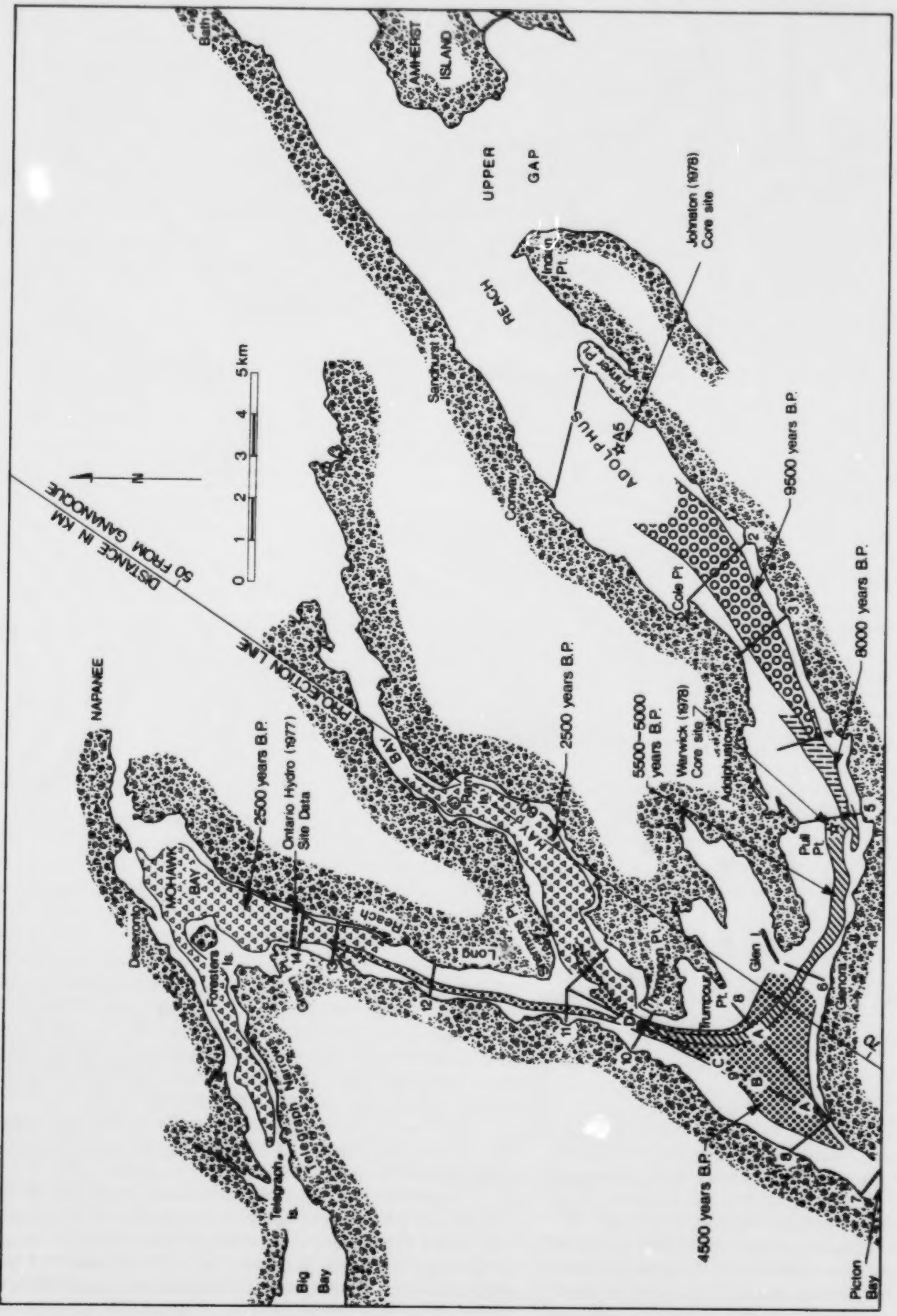
FIG. 2. Postglacial changes of lake level in the Lake Ontario basin.

on the Mountain, Roblin Lake, Rossmore Bog, and Big Swamp (Prince Edward County) are likely remnants of preglacial and interglacial features (Terasmae and Mirynech 1964; Sly and Prior 1984).

Postglacial Evolution

At the end of the last glaciation, as ice retreated to the north and northeast of the Lake Ontario basin during the late Wisconsin stage, high-level Lake Iroquois (Coleman 1937; Karrow et al. 1961) spread into the Bay of Quinte and Kingston basin shortly after 12 500 B.P. (Terasmae 1980; Sly and Prior 1984; (Fig. 2.). For a while, glacio-lacustrine clays were deposited and high-level beach deposits were formed. However, within a few hundred years, the ice that blocked the outlet from the Ontario basin eastward through the St. Lawrence Valley is thought to have begun further retreat (Sly and Prior 1984), and Lake Iroquois water levels dropped. This resulted in the formation of lower beach levels of the Frontenac–Trenton lake phases (Mirynech 1962). Water levels continued to drop in the Ontario basin and reached the lowest level shortly after 12 000 B.P. Sedimentation probably began in early Lake Ontario during the Greatlakean advance (Dreimanis and Karrow 1972; Sly and Prior 1984), and there is evidence of ice distortion of earlier deposits in the Kingston basin (Sly and Prior 1984).

Despite continued isostatic recovery, the eastern end of the Lake Ontario basin remained more depressed than the western end (Clark and Persoage 1970; Kite 1972) and thus, at that time, only a small body of water was retained in the basin, at an elevation much below present lake level (Bowlby 1975; Sly and Prior 1984). The opening of the Kirkfield outlet, between about 11 500 and 11 200 B.P. (Karrow et al. 1975; Johnston 1978), produced a major discharge of Upper Great Lakes water through the Trent River directly into the head of the Bay of Quinte which was then above the main early Lake Ontario level. Many of the glacio-lacustrine clays, previously deposited in the Bay, were removed at this time, and some may have been replaced by


NAPANEE
Deseronto
MOHAWK BAY
Foresters Is.
Telegraph Is.
Telegraph Narrows
Big Bay
Picton Bay
2500 years B.P.
Ontario Hydro (1977) Site Data
Long Reach
HAY BAY
BAY
PROJECTION LINE
50 FROM GANANOQUE
DISTANCE IN KM
N
0 1 2 3 4 5km
2500 years B.P.
5500–5000 years B.P.
Warwick (1978) Core site
Adolphustown
Pull Pt.
Glen I.
Thompson Pt.
Glenora
4500 years B.P.
8000 years B.P.
9500 years B.P.
Cole Pt.
Conway
Sandhurst
ADOLPHUS
REACH
A5
Johnston (1978) Core site
Indian Pt.
UPPER GAP
AMHERST ISLAND
Bath
A
B
C
1
2
3
4
5
6
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13
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FIG. 3. Simulated postglacial flooding of the Bay of Quinte (acoustic and core location data).

TABLE 1. Subsurface acoustic penetration data (echosounding); transect lines on Fig. 3.

Transect line	Location	Water depth (m)	Thickness recent sediment (m)	Elevation at base of recent sediment (m) (a.s.l.)[a]
1	Centre 1–1.5 km	52.7 (max.)	Approx. 10	Approx. 11 (irregular bedrock or till subsurface)
2	Northern half of line	36.0 (max.)	Uncertain but possible about 10	26–28 (bedrock or till surface)
	Southern half of line	38.0 (max.)		
3	Deepest part	39.3	10–11	23–24 (irregular bedrock or till subsurface)
4	Near deepest part	32.8	Nil	41.2 (surface cut into terrace deposit)
5	Just south of deepest part of line	22.0	3.5	48.5
	Nearer to south shore	21.0	5.0	48.0 (old fluvial channel)
6	100–200 m either side of max. depth	18–20	Nil	54–56 exposed bedrock surface
7	Deepest part	8.5	Uncertain	—
8	Fix point A, near NE end of line	11.3	6–7	55–56 (uncertain substrate below this subsurface)
	Approx. 0.5 km from SW end of line	11.0	3.5	59.5 (bedrock subsurface)
	Approx. 1.0 km SE from cement plant	9.1	2.5	62.4 (bedrock subsurface)
9	Fix point A	9.1	3.0	61.9 (uncertain substrate below this subsurface)
	Fix point B	10.0	3.0	61.0
	Fix point C	9.1	6.0	58.9
	Fix point D	15.2	6.0	52.8
	North end of line	6.5	5.0	62.5
10	Deepest point	15.2	5.0	53.8
	North of deepest point	7.6	4.5	61.9
11	Just west of Sherman Pt. buoy	6.7	6.3	61.0 (bedrock or till subsurface)
	Deepest part of Hay Bay entrance	10.7	6.0	57.3
	South side, Hay Bay entrance	7.9	5.0	61.1
12	Near midline	8.5	4.0	61.5
13	Deepest point	12.1	2.0	59.9 (old fluvial channel)
14	Deepest point	8.5	Uncertain	—

[a] Lake Ontario datum 74.0 m (a.s.l.). No distinction can be made between bedrock and glacial-till in most available echotrace data. The term "recent sediment" implies that all material is of postglacial age unless otherwise noted. There is a well-defined stratigraphic break within the recent sediments of the Bay of Quinte, often at a depth of 1–2 m. This probably represents the low level of early Lake Ontario. Modern sediments, above this surface, represent deposition under fluvio-lacustrine conditions and are associated with the last inundation of the Bay.

coarser fluviatile sediments (Coleman 1937). The sequence of events in the Lake Ontario basin following closure of the Kirkfield outlet is not clear, but shortly after 11 000 B.P. there appears to have been a late-glacial advance in the Ottawa–St. Lawrence area (Catto et al. 1981, 1982). Evidence of intense cooling is provided by thermokast ice-wedge structures preserved in shallow water sediments from the Kingston basin (Bowlby 1975; Sly and Prior 1984).

Postglacial conditions were well established by 10 500 B.P., and as a result of continued isostatic rebound, the diversion of Upper Great Lakes drainage away from Lake Erie became complete about 10 000 B.P. (Lewis 1969) and reduced the inflow to Lake Ontario (Sly 1983a, 1983b). Shortly afterwards, rising waters of the Kingston basin began to penetrate the lower reaches of the Bay of Quinte.

Johnston (1978) used the presence of a sand horizon in a core near the Brother Islands (Fig. 1) to show that the elevation of the Lower Gap control sill now lies about 25 m below lake level. Surveys of the Upper Gap put the depth of a bedrock sill at about 30 m below lake datum. The distance between sites projected onto a line N33°E (perpendicular to the present isobase) is about 16 km, and this implies a relative difference in isostatic recovery

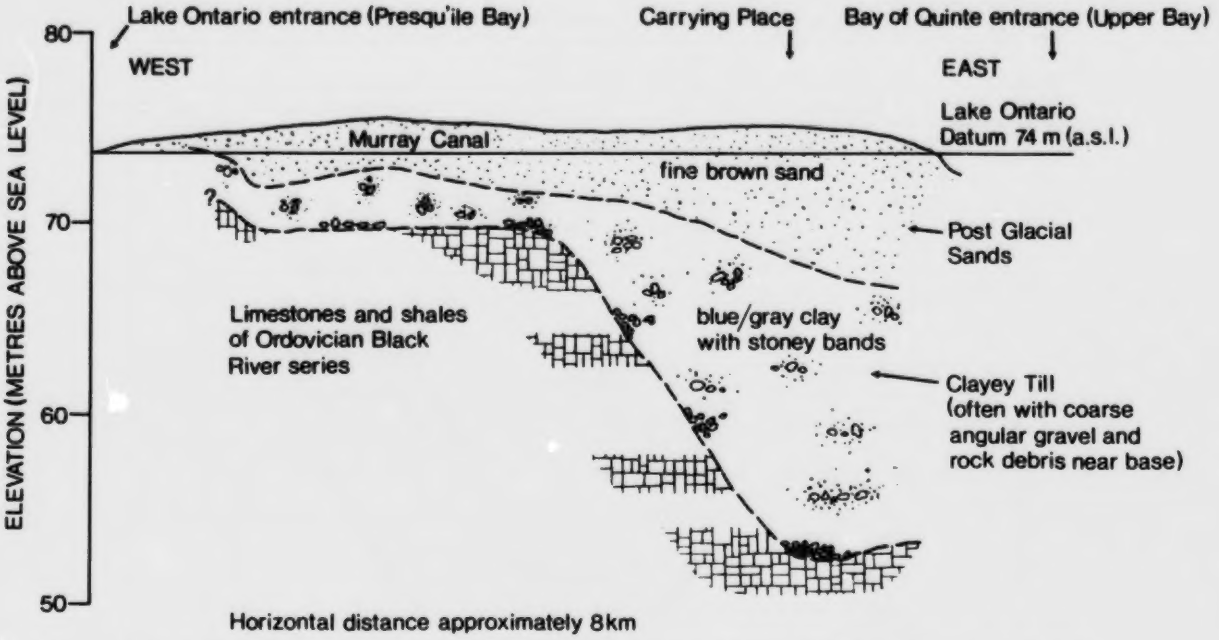


FIG. 4. Geological section of the Murray Canal (based on Ontario Ministry of the Environment borehole data).

of 5–6 m between the two sites (Sly and Prior 1984). The present elevations of the control sills therefore indicate that at the time of the lowest water levels in the Lake Ontario basin, following the fall of Lake Iroquois (Fig. 2), Bay of Quinte waters were ponded 15–20 m above the main lake. Bay waters extended back to between Cole Point and Keith Shoal (Fig. 3). The Upper Gap sill remained above the Kingston basin level until about 9500 B.P., and the Lower Gap was submerged a few hundred years later. As Lake Ontario continued to rise, lacustrine conditions extended upstream into the Bay of Quinte. Following the return of Upper Great Lakes drainage through Lake St. Clair, beginning about 5000 B.P. (Lewis 1969), water levels in the Lake Ontario basin probably made a stepwise adjustment of level (Johnston 1978). A simulated inundation of the Bay of Quinte, based on Sly and Prior (1984) and data on Table 1, indicates how continued uplift of the Lake Ontario control sill, east of Kingston, has caused the most recent flooding of Hay Bay and an overtopping of the secondary control sill at Telegraph Narrows (Fig. 3).

Published information gives little indication about the form and probable outlet of the early Bay of Quinte; and since bedrock is not exposed west of the Bay along the route of the Murray Canal (Haefeli 1972), it might be supposed that at one time there was a western outlet to the Bay. Unpublished engineering records from the construction of the Murray Canal (Parks Canada) indicate, however, that there is a generally thin cover of recent sediment over glacial till. Ontario Ministry of Environment well boring data (Fig. 4) show that glacial till fills most of the depression west of Trenton and that this is covered by overlying lacustrine sands which likely predate the last low-level stage in the Ontario basin. Thus, it seems reasonable that drainage from the Bay of Quinte passed into the Kingston basin following formation of early Lake Ontario (11 500 B.P.). This is further supported by effects of isostatic recovery which clearly indicate that the eastern end of the Bay of Quinte has been rising more rapidly than the western end (Clark and Persoage 1970; Kite 1972). The general lack of supply of recent sediments to Presqu'ile Bay, from sources to the east of Brighton, is entirely compatible with the distribution and transport of modern sediments in Lake Ontario (Rukavina 1970) which are largely derived from sources to the south and west of Brighton.

Significance of Geological Changes

Inundation has caused major long-term changes in the surface area, volume, and circulation of the Bay of Quinte, it has caused changes in the types and quantities of aquatic vegetation, and, in particular, it has caused changes in the type and distribution of bottom sediments at the mouths of streams and creeks. There is a tendency for course deposits to be covered by finer materials. Increased sediment runoff caused by modern settlement has likely accelerated rates of sediment accumulation in many parts of the Bay.

The Bay provides a wide variety of habitats for fish spawning. For example, the outcropping of the Sherman Fall Unit which is composed of bands of hard limestone, claystone, and fragmented limestone (Liberty 1961a, 1961b) is a preferred surface for spawning whitefish (Hart 1930) because of its shallow depth. Other shallow water sites include the Makatewis Island Shoal (near Trenton), Hog's Back Shoal (north of Big Island), Telegraph Narrows, and the Ram Island Shoal. Many of these sites would not have been available for spawning whitefish even a few thousand years ago. Their present suitability must obviously depend upon the depth of water, although numerous other factors also influence successful reproduction.

Although water level changes have had a major influence upon the long-term development of habitat in the Bay of Quinte, isostatic recovery during the past 200 yr or so has accounted for less than 0.2 m increase in water depth. Compared with the effects of climatic variation and cultural impact, recently rising water levels have had a less obvious effect on environmental change in the area.

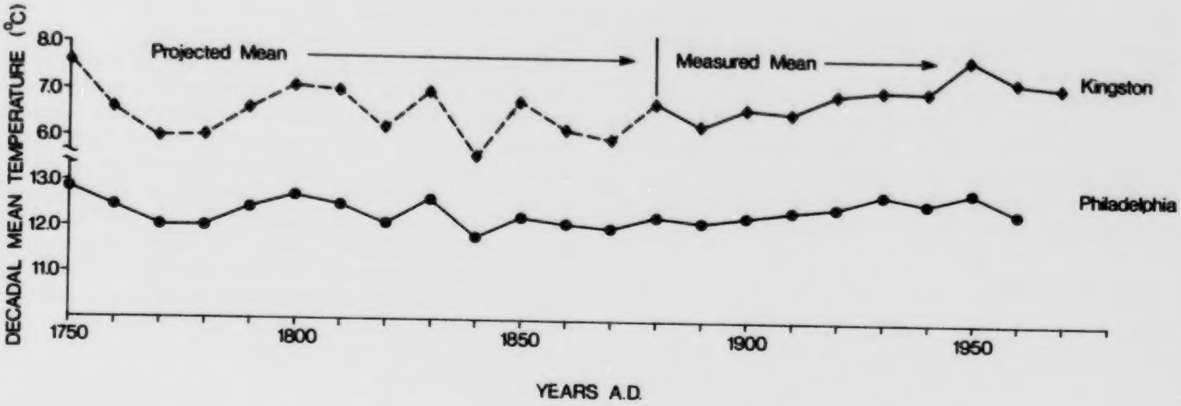


FIG. 5. Comparison of Philadelphia and Kingston temperatures since 1750.

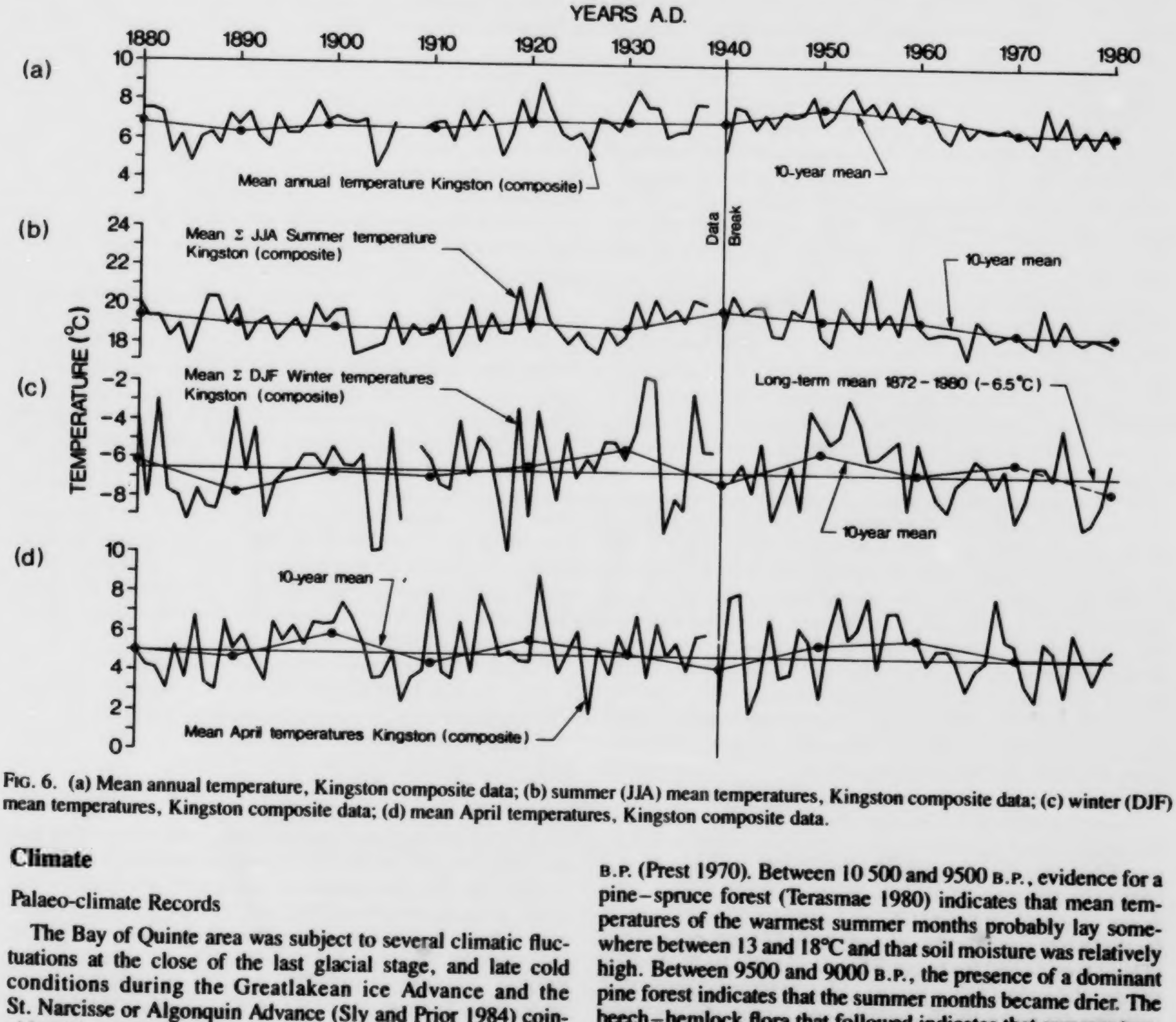


FIG. 6. (a) Mean annual temperature, Kingston composite data; (b) summer (JJA) mean temperatures, Kingston composite data; (c) winter (DJF) mean temperatures, Kingston composite data; (d) mean April temperatures, Kingston composite data.

Climate

Palaeo-climate Records

The Bay of Quinte area was subject to several climatic fluctuations at the close of the last glacial stage, and late cold conditions during the Greatlakean ice Advance and the St. Narcisse or Algonquin Advance (Sly and Prior 1984) coincide with similar hemispheric cooling in Europe (Lamb 1977).

Pollen records confirm the effects of global warming trends after about 10 000 B.P. which may have been modified by a temporary short cooling during the Cochrane Advance ca. 9000 B.P. (Prest 1970). Between 10 500 and 9500 B.P., evidence for a pine–spruce forest (Terasmae 1980) indicates that mean temperatures of the warmest summer months probably lay somewhere between 13 and 18°C and that soil moisture was relatively high. Between 9500 and 9000 B.P., the presence of a dominant pine forest indicates that the summer months became drier. The beech–hemlock flora that followed indicates that summer temperatures likely increased, but more specifically that the winters were milder and with few late spring frosts. The beech–hemlock zone coincides closely with the Hypsithermal climatic optimum between ca. 8000 and 4000 yr B.P.; and this zone reappears during the period between ca. 2500 and 1000 B.P. when warmer temperatures again characterized hemispheric conditions (Lamb 1977).

Between ca. 1400 and 1550 A.D. and ca. 1650 and 1850 A.D., the Bay of Quinte area was influenced by a marked cooling during the "Little-Ice Age" which affected much of the Northern Hemisphere (Thomas 1968; Lamb 1977). During this episode, beech pollen descreased markedly, and both pine and birch pollen increased in relative importance (Terasmae 1980).

Recorded Temperatures

Early records of climatic data began at Philadelphia, PA, in 1738 A.D.; records at Toronto began in 1840 and at Kingston during the 1870's. Before 1780, few regularly recorded data are available in eastern North America, occasional records are usually available in a diary form, and these often describe only unusual events. Event data indicate that the winters of 1691 and 1692 were much colder than normal in both eastern North America and Europe (Stommel and Stommel 1979; Matossian 1982). Canniff (1971) cited repeated crop failures in Lower Canada as evidence of poor weather during the 1750's, although other factors may have been involved. Crop failures were noted in 1783–84 (Stommel and Stommel 1979) and in 1787, and a hard winter in 1788 (Canniff 1971). A particularly cold summer was noted in 1816 (Stommel and Stommel 1979), but unusually mild winters with little snow occurred during the 1820's (Moira River conservation Report 1950). Most recently, severe winter conditions have been experienced in 1933–34, 1977–78, and 1981–82.

Unweighted decadal mean temperatures at Philadelphia provide a good indication of long-term temperature trends in eastern North America since about 1750 (Lamb 1977), and unweighted decadal means at Kingston (1880–1960) share similar trends. Correlations of $r = 0.78$ and 0.83 for data sets having medians finishing 1960 and 1965, respectively, are significant (1% critical value is 0.74). Although variation about the mean at Kingston is about twice that at Philadelphia, for the 1880–1960 temperature series, trends in the data are remarkably similar. Based on this relationship, the decadal means at Kingston have been projected back to the 1750's (Fig. 5). The projected data suggest that the Quinte area may have experienced significantly lower than normal temperatures during the decades of 1770, 1780, 1820, 1840, and 1870. Recent spruce tree ring width data from northern Quebec indicate poor growth conditions between 1770 and 1790 and 1820 and 1840 (Payette et al. 1985). Improved growth conditions ca. 1740, 1800–10, and 1850, also seem to be generally reflected in the projected Kingston temperature series. Temperatures since 1900 have been generally warmer than the previous 150 yr; a maximum mean temperature was reached during the 1950 decade.

Trenton airport and Kingston airport data have been normalized to Queen's University data to produce a nearly continuous data series for the period 1880–1980. These Kingston composite data are used (Fig. 6a–6c) to illustrate changes in the means of annual, summer (JJA), and winter (DJF) temperatures for the Quinte area. The data provide an insight into the structure of long-term annual temperature trends and show that, although the decadal annual mean peaked about 1950, low winter temperatures during the 1940's clearly supressed the influence of the summer high which peaked about 1940. Winter temperatures show greater variation about the mean than summer temperatures. April temperatures, as a correlate of spring melting, also show considerable year to year variation (Fig. 6d).

Recorded Precipitation

Mean annual, summer (JJA), and winter (DJFM) total precipitations are presented (Fig. 7a–7c) as Kingston composite data in which March data have been included to accentuate the potential source of water available for spring runoff. Major variations in the annual precipitation occur throughout the data set, but there is a significant peak in the decade about 1950. The decadal mean summer precipitation (190–235 mm) shows little departure from the long-term mean. The range of decadal means of winter precipitation lie between 200 and 320 mm, and although there is little variation about the long-term mean, it is greater than observed in the summer data. Periods of low winter precipitation occurred between 1910 and 1930 and again between 1960 and 1970.

Significance of Climatic Change and Variation

Changes in the long-term trends of mean annual and seasonal tempartures will have direct impact upon primary and secondary production, species composition, and reproductive success of most taxa in the Bay. Temperature changes may be sufficient, also, to affect settlement and agricultural activities in the watershed and therefore, indirectly, to affect loadings to the Bay. Post-glacial climate changes had a dramatic effect upon the terrestrial vegetation around the Bay, and during the past 50 yr, mean annual temperatures have been probably as warm as at any time during the past 2500 yr. Even though long-term recorded climate appears to be relatively stable, short-term fluctuations and events may cause significant environmental impacts.

Spring to midsummer spawning conditions are particularly important for a number of fish species such as walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), and white perch (*Morone americana*). Warm April and May temperatures, during the years identified in Fig. 8, probably enhanced successful hatch and increased the availability of zooplankton which support initial feeding. On the other hand, cold early summer temperatures, especially since the early 1960's, have likely had an adverse effect upon the white perch population which is near the northern limit of the species range (Scott and Crossman 1973). Combined temperature conditions are also important for some species, such as the whitefish (Christie 1963; Christie and Regier 1973), which could have benefitted from the cold fall/warm spring thermal index values identified in Fig. 8.

Kingston decadal precipitation data show good correlation ($r = 0.75$) with Lake Ontario water levels between 1880 and 1980, although year to year correlation is poor (Fig. 9). The maximum range of water level variation is about 1.5 m with high periods between 1882 and 1891, 1903 and 1920, 1927 and 1930, and 1942 and 1957. During these periods the increased water levels may have modified water quality in the Upper Bay by increasing the volume and could have changed the use of fish spawning habitats and the structure of wetland areas.

Although the combination of high winter precipitation and warm spring temperatures (Fig. 6d, 7c, and 8) has occurred several times in the past century, the only years in which there appear to be links between temperature, precipitation, and flooding are 1886 and 1936. The cause of spring floods on the Moira River in 1816, 1844, and 1868 is uncertain but floods in 1885 and 1981 were due to ice-jams (Moira River Conservation Report 1950). Comparison of flood data from the Trent River (Lower Trent Region Conservation Report 1970) and the Napanee River (Napanee River Conservation Report 1957)

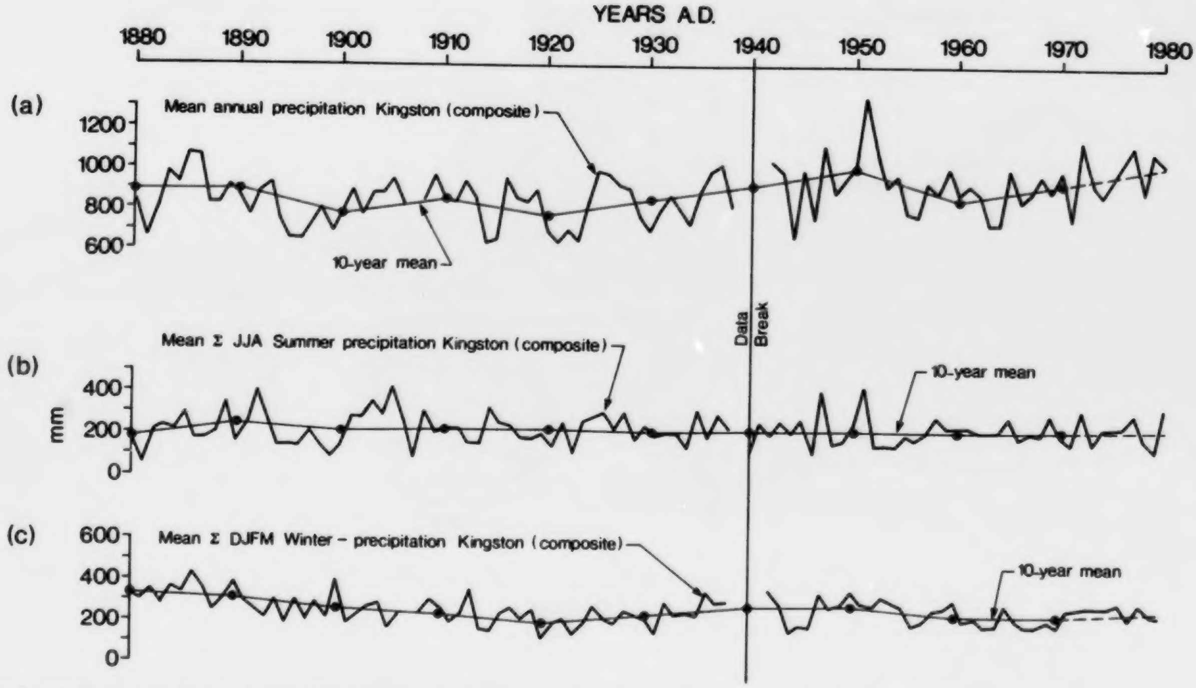


FIG. 7. (a) Mean annual precipitation, Kingston composite data; (b) sum of summer (JJA) mean precipitation, Kingston composite data; (c) sum of winter and early spring (DJFM) mean precipitation, Kingston composite data.

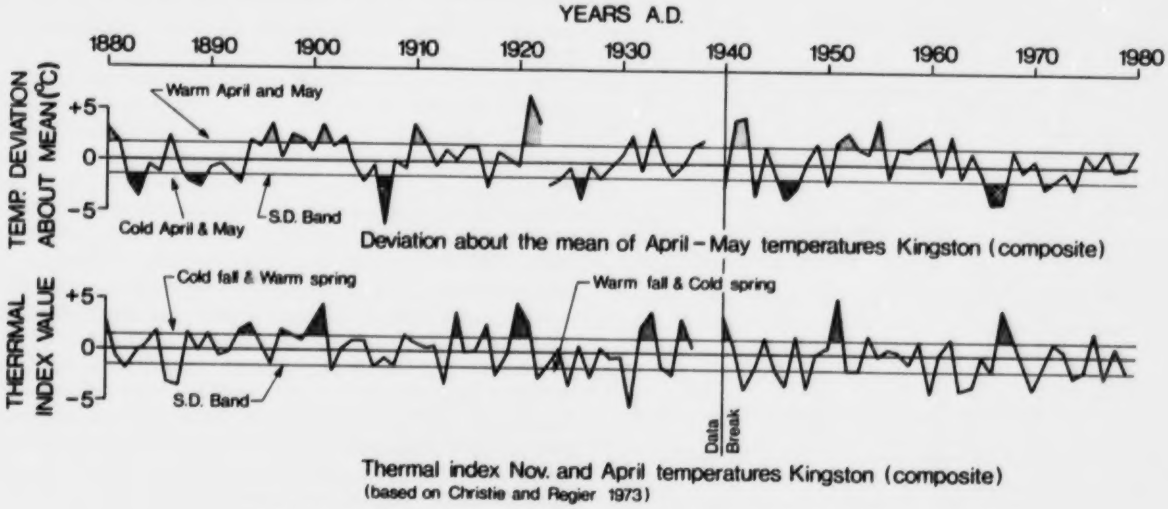


FIG. 8. April and May temperature deviations, Kingston composite data.

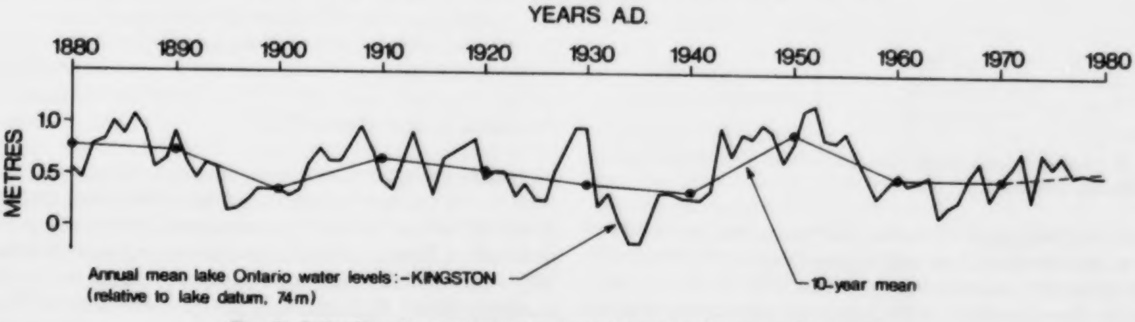


FIG. 9. Lake Ontario recorded water levels (Canadian Hydrographic Service).

TABLE 2. Drainage area and flows for specified periods of major rivers discharging into the Bay of Quinte.

	River				Remarks
	Trent	Moira	Salmon	Napanee	
Area (km^2)	12 940	2840	900	840	
Annual mean flow (m$^3 \cdot$ s^{-1}) predicted from area discharge (Ongley 1973)	122	27.2	84.7	8.1	
Annual mean flow (m$^3 \cdot$ s^{-1}), measured	90.1	29.9	—	9.1	
Maximum mean daily flow (m$^3 \cdot$ s^{-1}), measured	567	351	104	96	Floods
Maximum mean monthly flow (m$^3 \cdot$ s^{-1}), April, measured	206	116	—	37	High spring flow
Minimum mean summer flow (m$^3 \cdot$ s^{-1}), July–September, measured	36.8	5.4	—	1.7	Low flow

NOTE: Measured flow data from Inland Waters Directorate, Environment Canada; gauge station records at lowest point on rivers.

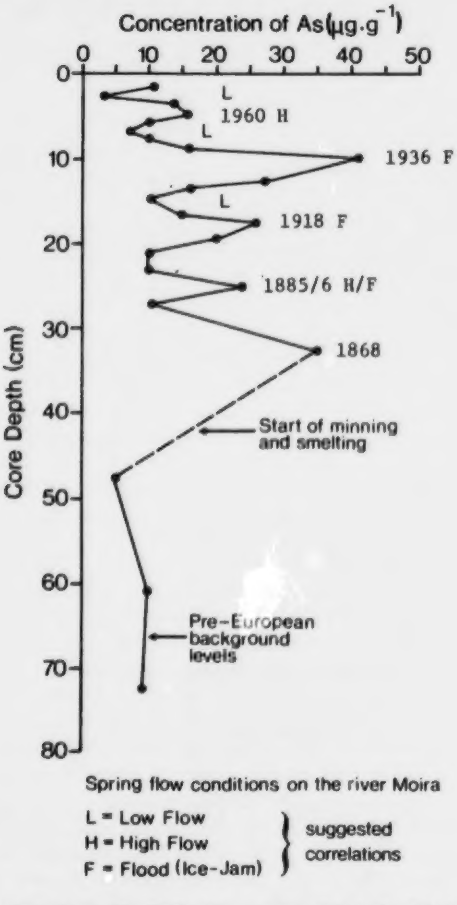


FIG. 10. Arsenic profile, Belleville core (modified after Mudroch and Capobianco 1980).

shows that flooding on these two rivers was usually less severe than on the Moira and that, with the exception of 1886 and 1936, none of the river flood years coincided. Environment Canada data for these rivers show that a general relationship between flow and seasonal precipitation exists, and that peak discharge is not synchronous in the basins. Spring runoff into the Bay of Quinte peaks in April, but because of pulsed inputs from different parts of the entire watershed, it can be spread over several weeks. Although the predicted mean annual flow of the Trent River is about 4.5 times that of the Moira (and about 15 times that of the Napanee), the measured peak month discharge of the Trent (April) is less than double that of the Moira River (Table 2). Thus, the Moira has its greatest impact on the Bay during the spring. Sediment discharge loads to the Bay are also greatest during the spring (Ongley 1973).

In a study of the impact of mining and smelting in the watershed of the Moira River, Mudroch and Capobianco (1980) described the presence of heavy metals in a core near Belleville (Fig. 1). The profile of As, a principal contaminant, is shown in Fig. 10. The core profile was dated using the *ambrosia* rise (ca. 1850 A.D.) at a depth of 22 cm; however, this was not reliable (A. Mudroch, NWRI, Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ont. L7R 4A6, pers. comm.). The initial increase of As, above background levels, occurred at some core depth between 33 and 47 cm and relates to the start of mining at Eldorado in 1866. Mining (As) in the Moira watershed ceased with the closure of the Deloro operations in 1961. It is believed that peaks in As concentration, down the core, may represent sediments which were flushed out of temporary upstream accumulations under high flow conditions. Some may coincide with flood conditions at the river mouth. Possible correlations are suggested against the profile.

Since low precipitation would result in low flow and reduced flushing rates and an increased concentration of nutrient loads, low summer precipitation may have caused the largest natural impact on trophic conditions in the Bay in recent years. Summer flushing is dominated by the flow of the Trent River (Table 2).

Settlement and Population

Indian artifacts recovered in the area of the Bay of Quinte indicate the presence of small nomadic populations from at least 4500–5000 B.P. Most settlements appear to have been on the west side of Prince Edward County (likely near Carrying Place), although there may have been some settlement on the lower Napanee River (J. Immerseel, Ontario Ministry of Natural Resources, Napanee, Ont. K7R 3S3, pers. comm.).

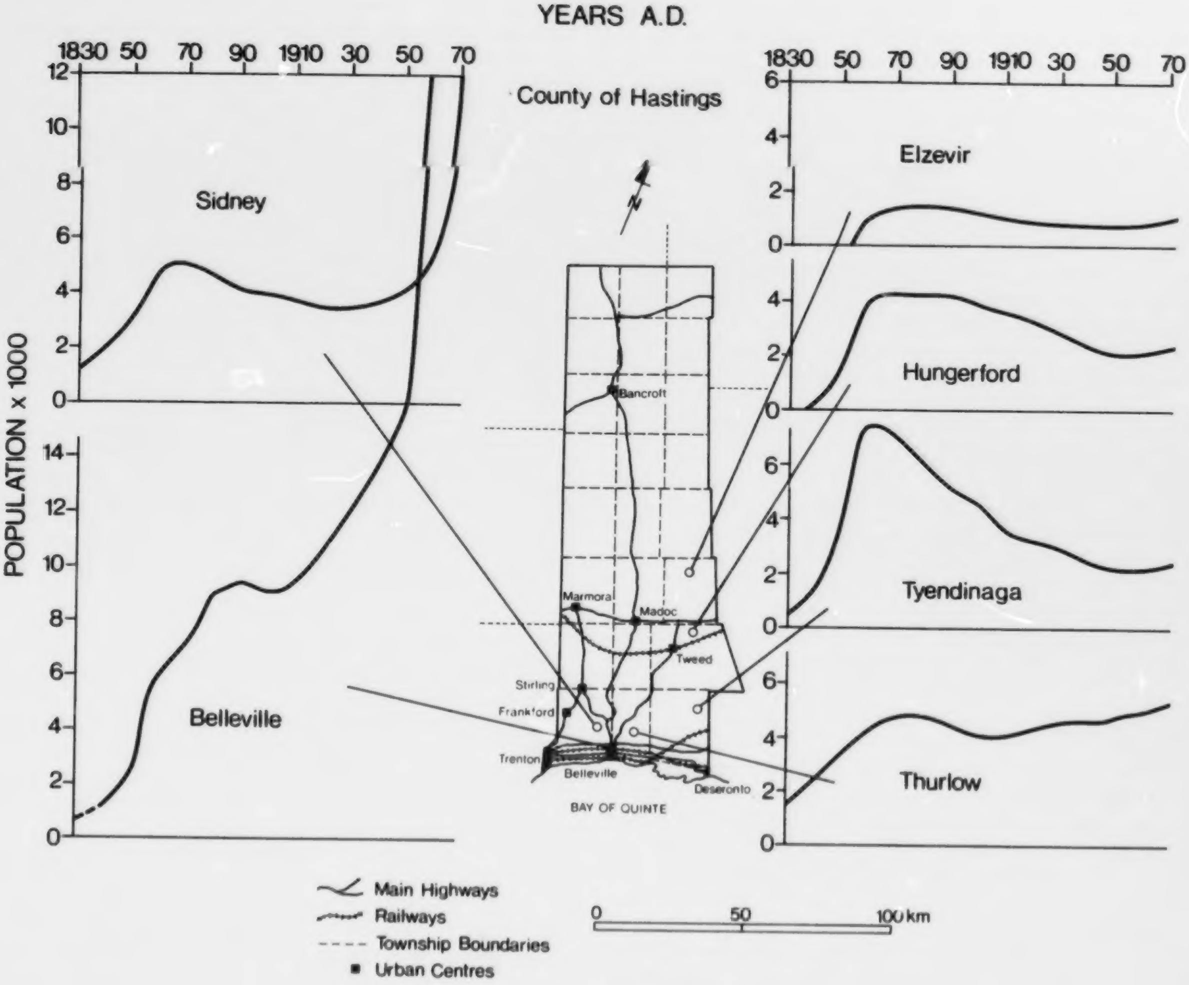


FIG. 11. Hastings County townships and population changes.

The first settlement by Europeans was made by the French Sulpician Order in 1668 (thought to be near Consecon, or Carrying Place), and a small Jesuit mission was established near the mouth of the Napanee River (Canniff 1971). The sites were abandoned in 1682.

Permanent settlement by Europeans, around the Bay, began towards the end of the American Revolution. In 1783, land between Trenton and Cornwall was purchased from the Mississauga Indians, and several hundred people moved into the area. Early development took place along the shoreline and it was not until after the mid-1820's that land grants and reforms encouraged penetration of the hinterland. The population around the Bay increased from 2000 in the early 1790's to about 90 000 at the turn of the nineteenth century, and to about 230 000 at present (CORTS 1975). The population development in townships and cities followed different courses (Fig. 11). For example, the settlement of Thurlow Township (around Belleville) began about 1790 and extended into Hungerford Township by 1835, and into Elzevier Township shortly after 1850. Following depletion of timer resources, populations in townships decreased although this was sometimes modified by the start of mining and quarrying such as occurred around Tweed (1890) and Marlbank (1900). The townships of Tyendinaga and Elzevier, however, lost two thirds of their populations in the 50–60 yr following their peak. This contrasts strongly with the population growth of urban centres such as Belleville where, apart from a slight decreased between 1890 and 1910, population has increased continuously.

Impact of Settlement Patterns and Population

Although Indian settlement around the Bay began during the Hypsithermal Period, and probably increased at the start of the climatic downturn about 600 B.P., there is no evidence of large and permanent communities prior to European settlement. Because later cultures also preferred bluff sites for the security of their fortified communities (Wright 1972), it seems unlikely that Indian settlements had much effect on water quality in the Bay, although there may have been other impacts associated with local forest clearance, hunting, and harvesting. The earliest European settlement could not have made much additional impact on the Bay, and in the years between 1682 and 1783 there was no habitation at all in the area because of the fighting between Indian tribes (Canniff 1971).

European settlement took hold in the area after 1783, with an immediate effect on the shore zone and aquatic resources of the Bay; settlement well inland of the Bay shore, however, did not become important for another 50 yr. Considering the close priximity of many settlements to the water and the rapid increase in population at the start of the nineteenth century, it is surprising that, although there were problems with sanitation and the supply of drinking water, degradation of water quality remained localized and did not become a Bay-wide problem until well into the twenthieth century. Because degradation of water quality was local, the availability of alternative habitats within the Bay provided a buffer for many fish stocks which were, therefore, not excessively stressed until well into the twenthieth century. It is not known if increasingly eutrophic conditions reduced macrophyte cover in the Upper Bay, but carp, which are potentially destructive of macrophytes (Baumann et al. 1974) and which were present during the early 1900's (McCrimmon 1968), were not abundant until the 1950's (Hurley and Christie 1977).

More than 50% of the population of the townships fronting onto the Bay is contained in five municipalities (Trenton, Belleville, Desoronto, Napanee, and Picton), and because of urban concentration, contamination has been strongly influenced by the character of point-source discharge. Although a change from dispersed septic systems to centralized treatment began about 1890 (C.L. Schelske, Great Lakes Research Division, University of Michigan, Ann Arbor, MI 48109, pers. comm.), at the larger urban centres, it may have caused an increase in nutrient loading to the Bay. This is because these municipal facilities provided only primary treatment. However, the introduction of high-phosphate detergents (1940's–50's) undoubtedly made the greatest impact on nutrient loadings (Johnson and Owen 1970).

Agriculture

The earliest agricultural activities in the area likely involved harvesting of wild rice, and the cultivation of Indian gardens was noted by Samuel de Champlain during his journey (1615) down the Trent River (Hannon 1971). Early European practices were introduced by the Sulpicians about 1668 but lasted only until 1682.

There was an explosive increase in agriculture with the arrival of the United Empire Loyalists in 1783, and during the 1820–30 period there was a shift from subsistence farming to commercial agriculture. Land clearance in the front townships was essentially complete by 1835 (Boyce 1967; Canniff 1971). Between 1861 and 1865, the American Civil War created an enormous export demand, particularly for wheat and dairy produce. Barley and hops became important in the 1840's and grew to dominate the market during the "Barley Years" (1860–90). Subsequently, agriculture has become more diversified.

Agricultural Impacts

The greatest impact from early European agriculture around the Bay was the increase in sediment loading and runoff as land clearance took place. Potash was available in plentiful supply, and later, small quantities of phosphate was available from Leeds County near Kingston (A. Crowder, Department of Biology, Queen's University, Kingston, Ont. K7L 3N6, pers. comm.) and gypsum from Oswego (Moira River Conservation Report 1950). Despite the use of these fertilizers, heavy cereal cropping led to problems of soil exhaustion in the latter half of the nineteenth century, when resulting soil loss probably again added to the deteriorating state of the Bay waters. Later, increased fruit and vegetable growing required more intensive agriculture (probably with As-based sprays) although without noticeable degradation of water quality until the late 1940's to early 1950's. At this time the use of fertilizers increased and the use of DDT became widespread, and since many orchards were close to the Bay, runoff and stream inputs resulted in direct contaminant loadings. Most recently, increased corn production has led to the use of even more fertilizers. The average use of fertilizer in the Trent–Moira watershed is 4.7 kg $N \cdot ha^{-1}$, 2.3 kg $P_2O_5 \cdot ha^{-1}$, 5.3 kg $K_2O \cdot ha^{-1}$, which is below the Lake Ontario watershed average (PLUARG 1978); however, on the higher quality lands near the Bay of Quinte, fertilizer use is much greater, with applications in the range of 11–22 kg $P_2O_5 \cdot ha^{-1}$ and additional manure (PLUARG 1978).

The importance of nutrients in runoff to the Bay is modified by the lack of high-capability soils along much of the northeast shore of the Bay (Richards and Morwick 1948; CORTS 1975). In addition, the presence of marsh and wetland areas in the Upper Bay, the Napannee River, and Hay Bay acts as a buffer zone which reduces the effects of direct runoff. Further, because most of the Prince Edward County watershed drains to the southwest, its contribution of agricultural nutrients to the Bay is very limited. Thus, despite the small area of the Bay relative to the surrounding land, spring runoff is not likely to be a major contributor to the development of early phytoplankton blooms in the Bay.

Industrial and Commercial Development

History of Development

The earliest development around the Bay of Quinte took place at a number of small "colonizing sites." Sawmills and flour mills were established very shortly after initial settlement in Kingston (1782), Millhaven (1785), Napanee (1786), Glenora and Belleville (1790), and Trenton (1794) (Moira River Conservation Report 1950; Napanee River Conservation Report 1957; Prince Edward County Conservation Report 1968; Lower Trent Region Conservation Report 1970).

As an example of the development of mills and dams in the region, there were four woollen mills and nine grist mills and more than thirty sawmills in the watershed of the Napanee in 1860. The peak of mill construction occurred earliest on the Napanee watershed, and similar development did not take place until about 20 yr later in the Trent watershed; exploitation and development tended to move from east to west throughout the Bay of Quinte region.

The exploitation of timber in the Bay of Quinte watershed as a whole reached a peak of about 22 million board feet (1 board foot = 2.36 dm^3) between 1872 and 1873, when about 200 000 logs were driven down the Moira River, alone. The last log drive on the Napanee was in 1905, on the Moira in 1907, and on the Trent in 1920.

Land clearance around the Bay provided an immediate timber supply for housing, shipbuilding, heating fuel, and the furniture industry until well into the 1830's. After this date, most large quantities of timber were brought into the Bay from further inland. In 1826, the British Naval reserve of white pine was released and a substantial new source of timber entered the market (Lower 1973). Hardwoods were used in the production of potash fertilizer, and between 1860 and 1890 there was a major trade in squared timber (Moira River Conservation Report 1950; Lower Trent Region Conservation Report 1970).

The location of mineral deposits and the start of mining (Fig. 12) in the Bay of Quinte watershed followed somewhat behind the exploitation of timber. Mining and smelting in the Marmora–Deloro–Madoc area (about 50 km north of the Bay) provided an important incentive for the development of Belleville. Although most of the mining has now creased, heavy metals contamination associated with mining and smelting prac-

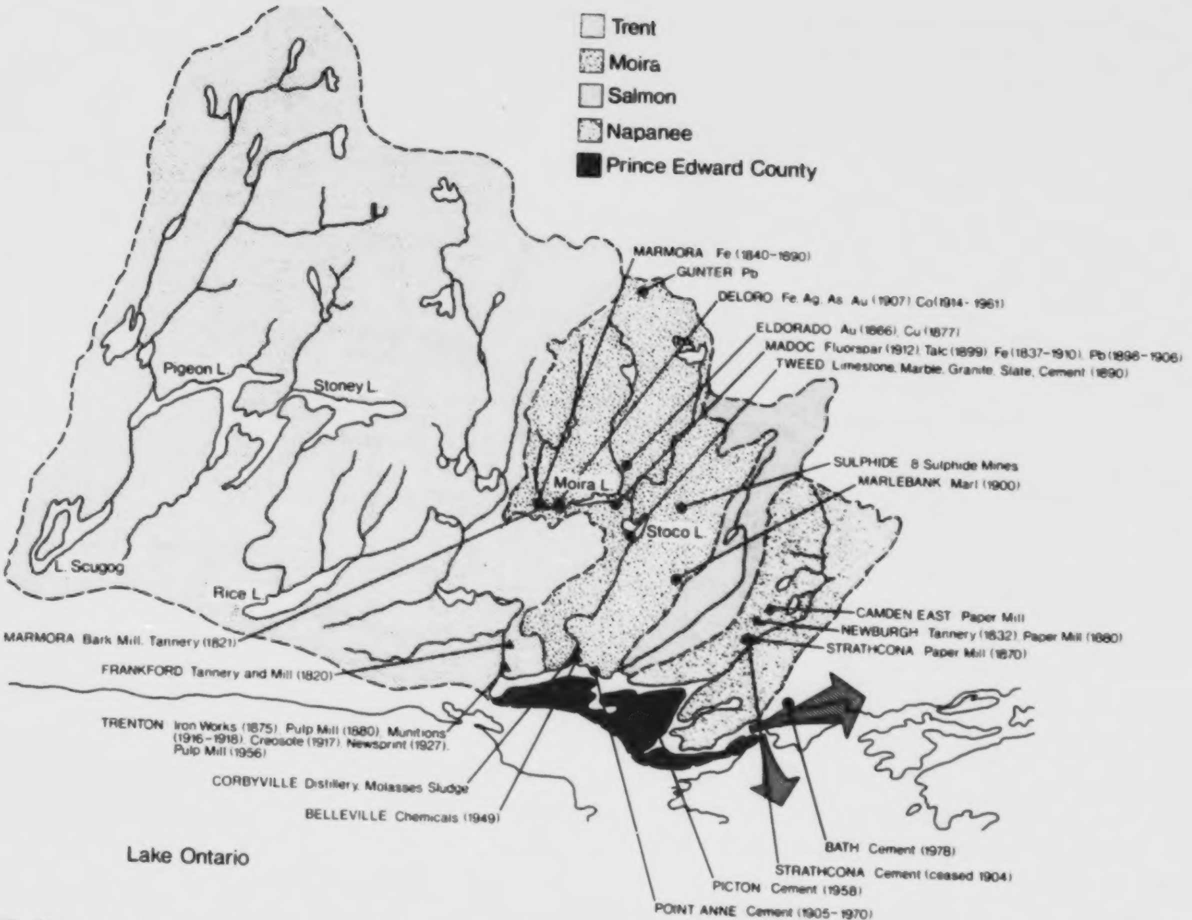

☐ Trent
▨ Moira
☐ Salmon
▨ Napanee
■ Prince Edward County
MARMORA Fe (1840–1890)
GUNTER Pb
DELORO Fe, Ag, As, Au (1907) Co (1914–1961)
ELDORADO Au (1866), Cu (1877)
MADOC Fluorspar (1912) Talc (1899) Fe (1837–1910), Pb (1898–1906)
TWEED Limestone, Marble, Granite, Slate, Cement (1890)
SULPHIDE 8 Sulphide Mines
MARLEBANK Marl (1900)
Pigeon L.
Stoney L.
Moira L.
Stoco L.
L. Scugog
Rice L.
CAMDEN EAST Paper Mill
NEWBURGH Tannery (1832) Paper Mill (1880)
STRATHCONA Paper Mill (1870)
MARMORA Bark Mill, Tannery (1821)
FRANKFORD Tannery and Mill (1820)
TRENTON Iron Works (1875), Pulp Mill (1880), Munitions (1916–1918), Creosote (1917), Newsprint (1927), Pulp Mill (1956)
CORBYVILLE Distillery, Molasses Sludge
BELLEVILLE Chemicals (1949)
Lake Ontario
BATH Cement (1978)
STRATHCONA Cement (ceased 1904)
PICTON Cement (1958)
POINT ANNE Cement (1905–1970)

FIG. 12. Minerals, mining, and quarrying in the Bay of Quinte watershed (modified after Moira River Conservation Report 1950; Napanee River Conservation Report 1957; Prince Edward County Conservation Report 1968; Lower Trent Region Conservation Report 1970).

tices and subsequent weathering of mine dump and tailings materials has been traced down the Moira system and into the sediments of the Upper Bay (Mudroch and Capobianco 1979, 1980). Quarrying for building stone began at Point Anne (Belleville) in the 1830's, and other sites were opened later around the Bay for the production of cement.

By the early 1820's the combined growth of road and water traffic (both sail and steam) favoured the development of regional centres at Trenton, Belleville, Napanee, Deseronto, and Picton. Over the years, the larger centres have developed a broad industrial base but most of the smaller centres such as Picton, Bath, and Sandhurst have become more dependent on single resource based industries (Lunn and Lunn 1967; Mika and Mika 1966, 1967, 1969, 1977).

Impact of Industrial and Commercial Activities

The construction of dams on the rivers and streams entering the Bay began in the 1780's, and by the 1830's there was a major decline in the Atlantic salmon (*Salmo salar*) fishery (Christie 1972). A power dam was built near the mouth of the Trent River in 1885 and the Corbyville dam was also built near the mouth of the Moira in the 1800's. The Trent canal system was started in the 1830's (completed 1918) and the principal impact of water level control in this system has been to regulate low flow conditions. The Murray Canal was started in the 1830's and opened in 1890. It has no locks and provides a small but direct exchange between Lake Ontario waters and the Upper Bay. This exchange appears to have little impact on sedimentation, but may benefit the Upper Bay (McCombie 1967) where water quality is similar to that of the inflowing Trent River (which also maintains the high flushing rate in the Upper Bay).

The Belleville–Rossmore bridge was constructed on open piles in 1891, but in the 1930's this structure was filled in to form a causeway. The causeway has restricted exchange in the Upper Bay, east and west of Belleville, and it has probably also caused sediments to accumulate off the mouth of the Moira River by providing protection from wave action. During the 1930's, Telegraph Narrows was blasted to a minimum depth of 3.3 m to allow better access for bulk carriers going to the Point Anne cement plant at Belleville. The blasting may have slightly increased exchange between Upper and Middle Bay waters, but otherwise, there appears to have been little effect. Wharf and harbour structures have continued to modify shoreline form and nearshore circulation in the Bay since the early 1800's, but have had little effect on circulation in the Bay as a whole.

Pulp mill effluents were contributed via both the Trent and Napanee rivers which, later, also contributed food processing wastes to the Bay. At the end of the nineteenth century, there were importance iron-works at both Trenton and Deseronto, and during the First World War, wastes entered the Bay from a munitions plant at Trenton. Timber wastes (bark and sawdust)

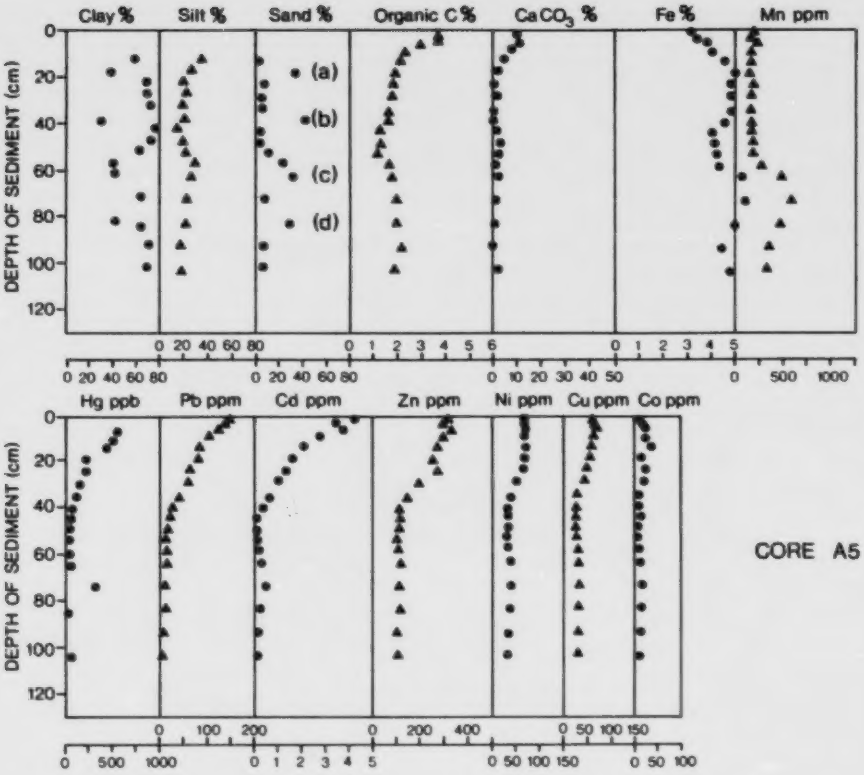


FIG. 13. Core A5 data (after Johnston 1978).

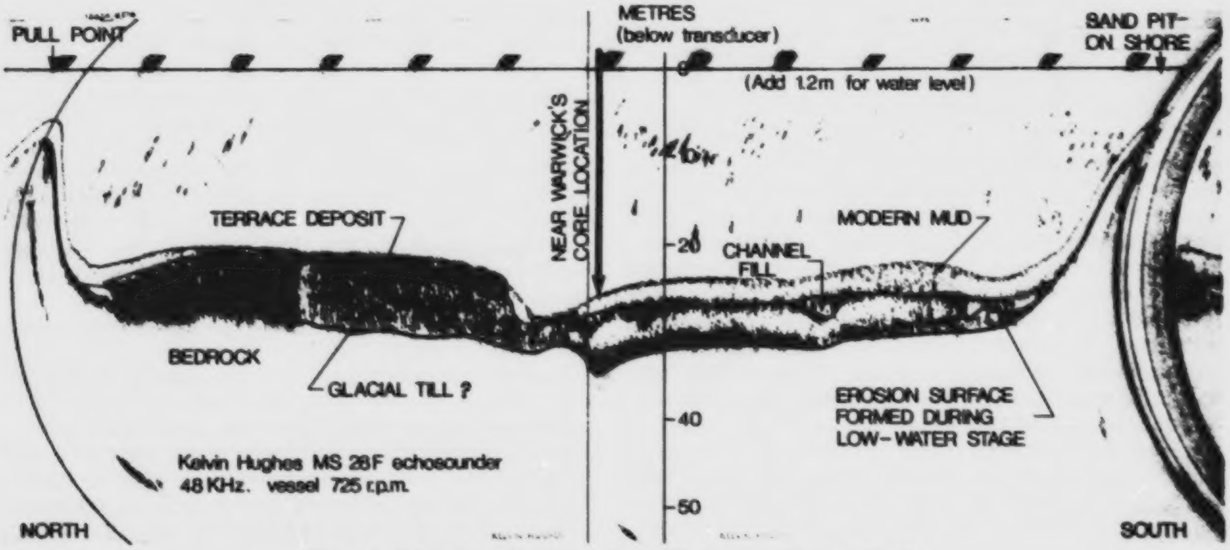
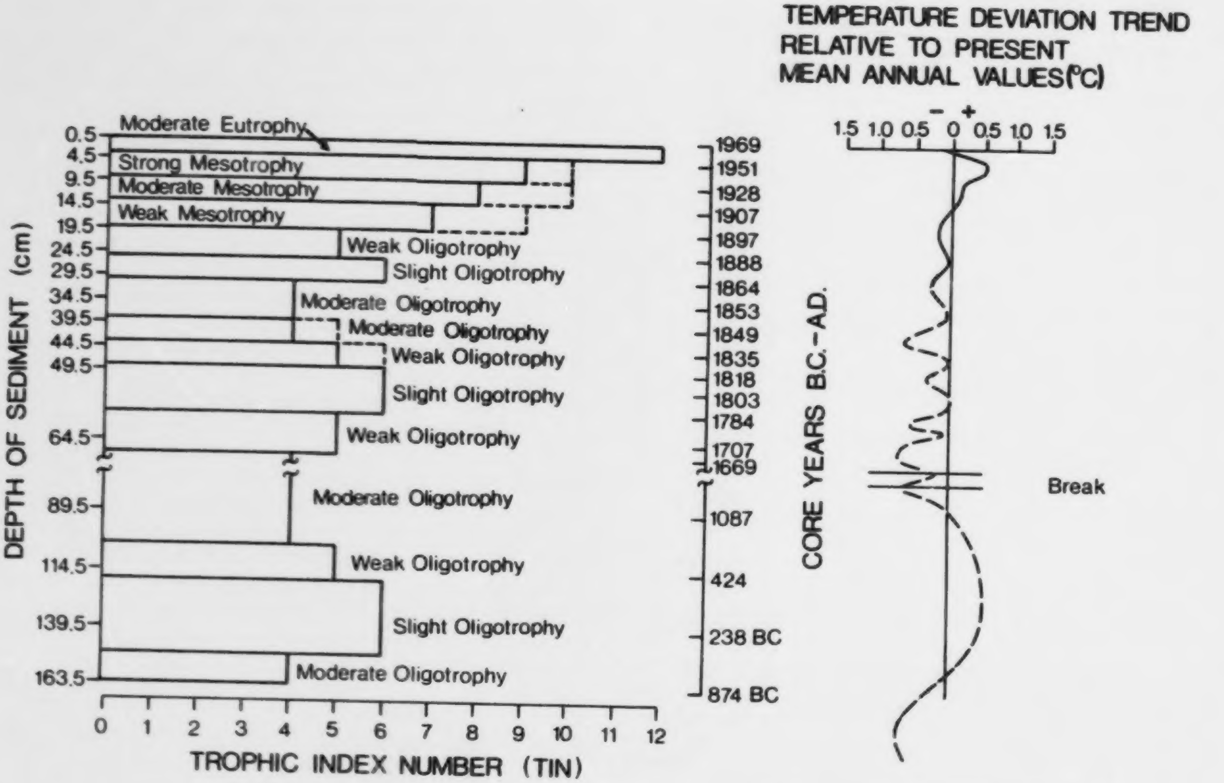

PULL POINT
METRES
(below transducer)
SAND PIT ON SHORE
(Add 1.2m for water level)
NEAR WARWICK'S CORE LOCATION
TERRACE DEPOSIT
MODERN MUD
CHANNEL FILL
BEDROCK
GLACIAL TILL ?
EROSION SURFACE FORMED DURING LOW-WATER STAGE
Kelvin Hughes MS 26F echosounder
48 KHz. vessel 725 r.p.m.
NORTH
SOUTH
0
10
20
40
50

FIG. 14. Echotrace section across Bay of Quinte near Glenora, line 5.

are known to have been a major contaminant in Bay waters, especially during the 1860's (Moira River Conservation Report 1950), but there is surprisingly little evidence of these wastes in modern sediment cores recovered from the Bay.

Wind-blown coal and, later, cement dust were probably introduced into the Upper Bay from the mid-1800's on, but largely ceased in the 1950's as plant closures took effect. Cement and coal dust are still occasionally blown into the Middle Bay from the cement plant at Picton which was opened 1958, but the dust is not deleterious to Bay-wide water quality (McCombie 1967). During the 1800's, fires were common in many communities and the largest known fire occurred at Deseronto in 1896 (Martin 1968); however, no evidence of this event has been found in sediment cores at downstream locations in the Bay.

Concentrations of arsenic are naturally high in the watershed of the Moira but mining and smelting activities over the past 100 years, and particularly since the late 1800's, have caused considerable elevations of the total arsenic content in water and sedi-



(Data, 1750 – present from fig. 5, data prior to 1750 based on hemispheric trends: Bryson et al. 1970, Lehmer 1970, and Lamb 1977).

FIG. 15. Trophic index number (TIN) (after Warwick 1978) and estimated yearly mean temperature data.

ment, throughout much of the Upper, Middle and Lower Bay (Mudroch and Capabianco 1979, 1980).

Core A5 (Fig. 3 and 13) from the Lower Bay (Johnston 1978) shows the influence of anthropogenic loadings in which the increases of many heavy metals (Cd, Hg, Pb, and Zn) appear to be strongly associated with increased organic carbon (OC) in the sediment (Sly 1984), reflecting contaminant/trophic state interactions within the Bay. Increased concentrations of calcium carbonate are also associated with OC and likely reflect increased precipitation of fine silt-size biogenic carbonate (Sly 1984). Recent increases in the concentrations of Co, Cu, and Ni in the Belleville (Mudroch and Capobianco 1980) and A5 core profiles are similar and indicate the extent to which fine sediments can be spread throughout the Bay. The As profile in the sediment core at Belleville differs greatly from those of Co, Cu, and Ni (Mudroch and Capobianco 1980). This is partly because of the later introduction of these metals into the Moira River (Evans et al. 1986), but more particularly because of the different geochemical behaviour of As and different particle-size associations (possibly related to mining processes). Because of relatively low flow velocities, however, variations (Fig. 13, a–d) in the sand content of core A5 probably indicate changes in local supply rather than effects of increased discharge in the Upper Bay. Data in Damiani and Thomas (1974) indicate the significance of sand as a high-energy material, within the Bay, and its limited distribution.

The presence of PCB's in Picton Bay and elsewhere in the Bay of Quinte (Frank et al. 1980) is an example of an important local source of contaminant such as may be derived from waste dump seepage or poor disposal practices. On the other hand, the presence of pentachlorophenols and their tetrachlorophenol degradation products, which have been found throughout much of the Bay in water, sediments, and fish, demonstrates the extent to which single source contaminants can spread within the environment. These contaminants have been traced to a wood preserving plant at Trenton which has been operating since the 1940's (Fox and Joshi 1984). The presence of persistent organic contaminants which include DDD, DDE, Lindane, Chlordane, and Mirex (Ontario Hydro 1977, 1978, and 1980) in sediment cores from the Long Reach (Fig. 3) indicates the most recent form of contaminent loading to the Bay, much of which is derived from multiple sources.

Generally, the effects of industrialization have been to deny stream access to migratory fish stocks, to modify summer flow of the Trent River, to contribute a wide range of contaminants, and to locally modify sediment accumulation patterns; of these, the impact of contaminants and resulting changes in water quality are of greatest concern.

Glenora-C Core

This core provides a unique source of data describing changes in the Bay of Quinte over the past 2800 yr. Because of this, information which relates particularly to changes in trophic state

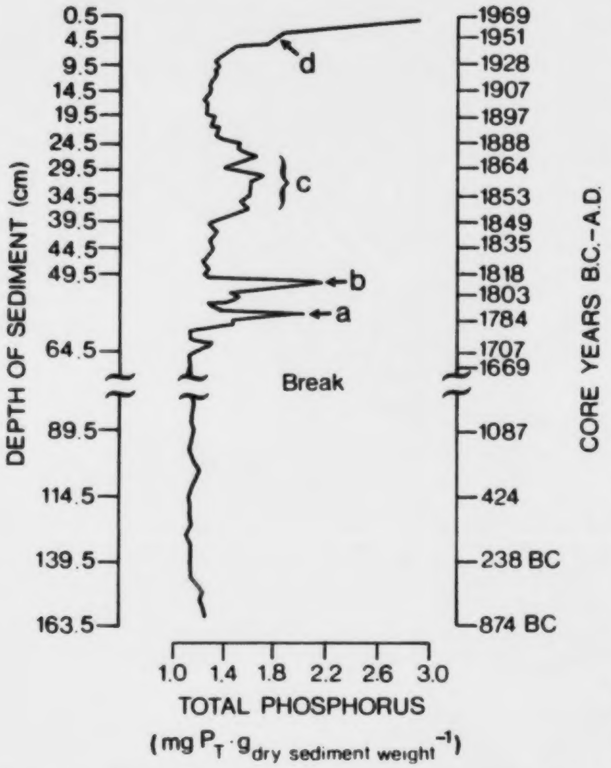


FIG. 16. Total P, Glenora-C core (modified after Warwick 1978).

is reviewed in the following discussion. Reinterpretation has been applied to some of the data. The core substantiates many of the points already made about the forms of natural and cultural impacts in the Bay.

Warwick (1978) recovered high-quality cores from a site near Glenora (Fig. 1) which have provided a remarkably detailed record of compositional changes to a depth of about 1.6 m below the sediment surface. In Fig. 14, an echotrace section across the Bay shows how the area of modern mud accumulation is largely restricted to the southern half of the section, and that modern muds overlie late glacial and postglacial deposits just below the base of Warwick's core. Lacustrine deposition under conditions of increasing water depth probably began about 5000–6000 B.P., and long-term average accumulation rates are about 0.6 mm · yr^{-1}; modern rates are very much higher (ca. 2.2 mm · yr^{-1}). Fox and Joshi (1984), in a nearby core, recorded modern rates of accumulation of as much as 8 ± 2 mm · yr^{-1}.

Nutrient Loadings and Biological Response

Warwick (1978) developed the trophic index number (TIN) based on analysis of benthic fauna composed largely of chironomid remains. He established different zones of trophic change in the Glenora-C core, and radiocarbon and lead-isotope dating techniques were applied to the sediments. In Fig. 15, Warwick's TIN data are compared with trends in long-term temperature around the Bay, based on recorded data (Kingston and Trenton, from 1872) and estimated data (Kingston, from the 1760's), and estimated hemispheric temperatures (Lamb 1977). The comparison suggests that trophic changes prior to the late 1800's can be largely accounted for by temperature change (which is entirely compatible with recent evidence derived from Lake Erie molluscan fauna; Kalas 1983a, 1983b). Warwick (1978) concluded that the natural range is between moderately oligotrophic and slightly oligotrophic at the Glenora site. The period of low trophic state conditions between ca. 1840 and 1860 appears to be anomalous. As suggested by Warwick (1978), it largely reflects the impact of increased sediment load (suppressed trophic conditions) which followed land clearance, although there may be some influence from temporary climatic cooling as well. The higher trophic states after about 1890–95 clearly imply the overriding effects of "cultural impact" (Warwick 1978).

In Fig. 16, the peaks *a* and *b* of total P probably reflect soil loss during periods of earliest land clearance at or near the Bay shore. Peak *b* appears to be coincident with an early record of flooding on the Moira River and may, therefore, also represent the effects of a very high flushing and runoff event. The less intense but longer duration P peak (*c*), between about 1850 and 1890, seems to coincide with the period of the "Barley Years" and probably indicates the impact of poor agricultural practices at that time. The last rise in total P began at the start of the 1930's, and a stepwise increase (*d*) can be noted in the early 1950's which coincides with the introduction of detergents.

The derivation of total P in peaks *a*, *b*, and *c*, from soil loss, is supported by the clay mineralogy data from Warwick's core. Warwick (1978) showed that montmorillonite is present in the upper parts of the core, but absent from subsamples in the lower parts. Montmorillonite is usually associated with Podzol A_2 soil horizons (Rutherford 1972) but not with glacial and glaciolacustrine deposits which are illite rich in the Lake Ontario basin (Thomas et al. 1972). This implies that, up until the early 1800's, most clay minerals were derived by bank erosion in the watershed but that, after this, surface wash and soil runoff contributed most of the sediment load.

The OC content in the Glenora-C core (Fig. 17) shows little correlation with the TIN until very recent time. However, this is not altogether surprising, since the TIN relates to in-place benthic conditions at Glenora, and it is not necessarily indicative of the trophic state elsewhere in the Bay. Similarly, although OC shows a continuous rise in the core after 1870, the rise in total P does not follow exactly the same trend. Thus, geochemical profiles in the sediments of Glenora-C core may not replicate the upstream nutrient loadings that were responsible for generating the plankton biomass recorded in the core. The C:N ratio in the Glenora-C core (Warwick 1978) increases with sediment depth (from < 7.5:1 to > 10:1), and is comparable with Lake Ontario core profile data (Kemp 1971). There is no evidence that either rooted aquatic plants or terrestrial vegetation (characterized by much higher C:N ratios; Boyd 1970; Kemp et al. 1972, 1977) contributed significantly to any part of the OC profile at this site. Thus, the core registers no indications of changes in macrophytes covers or loading of timber wastes which are thought to have occurred in the Upper Bay.

Erosion Index

Warwick (1978) used the erosion index (EI), defined as

$$\mathrm{EI} = \frac{\%\ \text{clay fraction} > 10.5\ \phi\ \text{size}}{\%\ \text{total clay fraction} > 8.5\ \phi\ \text{size}} \times 100,$$

to resolve subtle changes in core texture (Fig. 18). Generally, the EI increases with decreasing particle size (increases ϕ values). The EI should respond well to changing characteristics of the total received sediment load. However, because of the rapid dispersal of very fine materials in suspension, it is largely

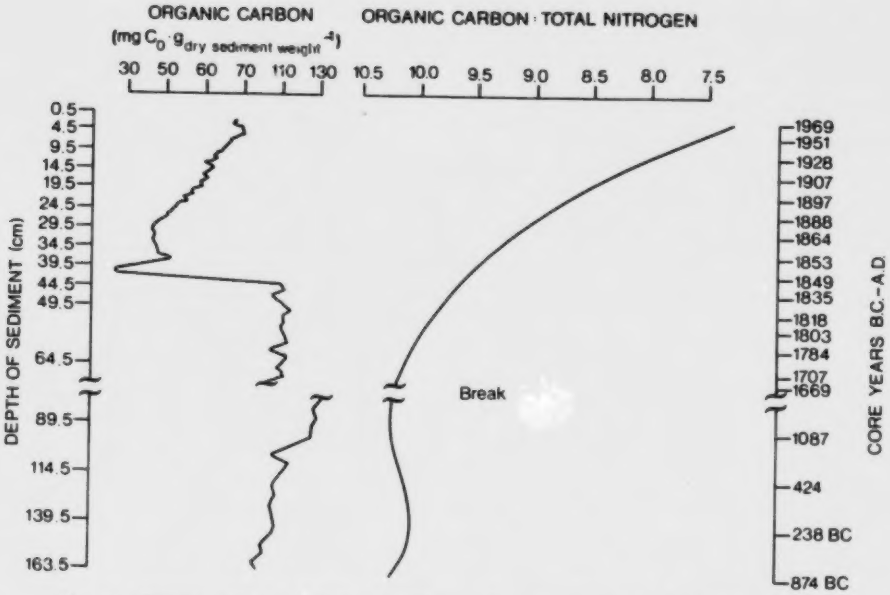


FIG. 17. Organic carbon and C:N ratio, Glenora-C core (modified after Warwick 1978).

insensitive to localized variations in input load, unless close to the source.

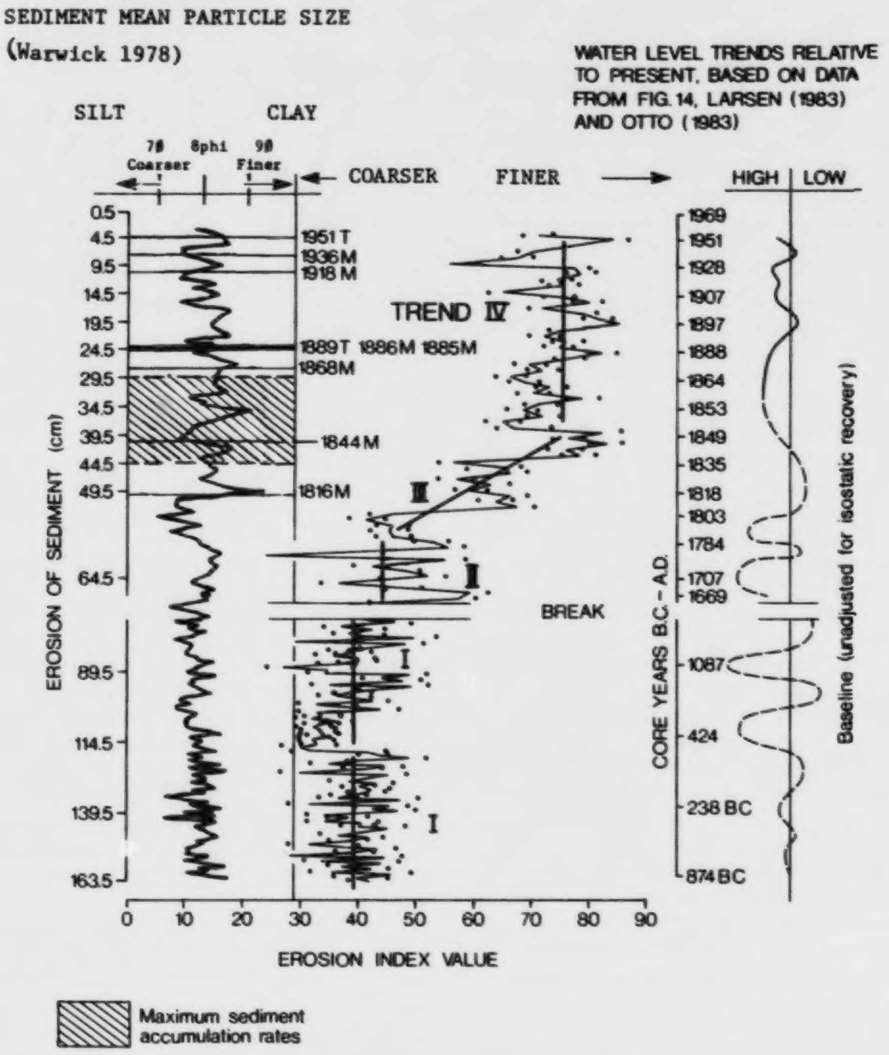
Based on simulated flooding of the Bay (Fig. 3), it is likely that overtopping of the Telegraph Narrows still took place at some time–depth interval near the base of the Glenora-C core; however, this is unlikely to have had much effect on the characteristics of sediments at the Glenora site, since the event marked only the inundation of a set of rapids which would have contributed nothing to the suspended load of the previous overflow. It is equally unlikely, before this, that the Telegraph Narrows posed a barrier to the transport of suspended sediments from Big Bay which, as now, must have been closely associated with wind-induced resuspension of bottom sediments and seasonal runoff under high flow conditions.

Four sets of trends (I–IV) are evident in the EI data of the Glenora-C core. Based on the interpretations by Warwick (1978), it is reasonable to presume that the break between trends II and III represents the change in sedimentation at the start of European settlement around the Bay. Thus, natural background conditions varied between 25 and 60 EI units. The principal cause of variations in trends I and II must be climatic, since no other factor could cause such large changes in composition of the integrated suspended load. It would seem, generally, that deposits of "coarse" material represent periods of high precipitation (cool–wet climate)and "fine" material represents periods of low precipitation (warm–dry climate). The dates of major changes correlate well with the climatic changes defined by Bryson et al. (1970) and Lehmer (1970) and the projected Kingston decadal temperature means (Fig. 5). This interpretation seems to be further supported by independent data from southern Lake Michigan where recent work by Larsen (1983) has detailed Holocene lake level fluctuations, based on stratigraphic evidence. Larsen's data have been combined with recent data from western Lake Ontario (Otto 1983 and unpubl. data) to provide a composite of lake level fluctuation trends which are shown alongside Warwick's EI data in Fig. 18. There is a noticeable break in trend I, at about A.D. 400 and this coincides with the first major water level excursion. Although there is considerable "noise" in the data, this and subsequent water level changes are well represented in the EI data series.

Trend II is characterized by large variations of the EI and a slight but noticeable shift towards "finer" mean particle size, but the meaning of these changes is unclear. The large variations of EI might be caused by changing forest cover (beech–hemlock to pine–birch) and excessive freeze–thaw weathering during periods of short climatic cooling (Fig. 15, ca. A.D. 1707 and 1784). The changes also could reflect cultural impact (Mississauga Indians) but such a source would have to be close to Glenora.

In trends III and IV, cultural impact is superimposed on the background of climatic change and dominates the shift in EI values. The fining of suspended load, indicated by increasing EI values in trend III, likely demonstrates the effects of deforestation and the influence of flow modifications in major watersheds of the Bay. Timing of this trend seems to coincide almost exactly with the construction of mills and dams on the Napanee River. Since the construction of major facilities on the Moira and Trent rivers after 1850's does not seem to be reflected in the Glenora-C core data, with the exception of extreme events, it is likely that sedimentation in Big Bay may largely buffer the downstream effects of short-term discharge variation from the Moira and Trent rivers.

Trend IV is characterized by a return to generally stable long-term EI values between 1865 and 1885, and indicates that the composition of suspended sediment at Glenora remains noticeably finer than during the precultural period. This could indicate a permanent increase in the proportion of very fine soil surface particulates in the sediment yield from the watershed, resulting from human land-use activities. However, since the exceptional peak in sediment accumulation rates (due to land clearance ca. 1840–65) seems to have had only a limited effect upon EI values (Fig. 18), it is likely that the principal cause of continuing high EI values is the presence of structures which limit stream flow and result in settlement of all but the finest particles. This interpretation is compatible with the behaviour of courser As-related particulates, noted in the Belleville core (Mudroch and Capobianco 1980), and the extensive dispersal of very fine Co- and Ni-related particulates which appear to show no con-



SUGGESTED EVENT CORRELATIONS

High Flow or Spring Flood Conditions - "year" M = Moira River

- "year" T = Trent River

FIG. 18. Erosion index (after Warwick 1978), water level trends, and mean particle size, Glenora C-core.

centration gradient in the Bay of Quinte, downstream from Belleville.

Cyclic periods of high water level are well reflected in the EI data, and it is likely that flooding of the Rossmore Bog took place during the mid-1800's. Terasmae and Mirynech (1964) recovered a shore core from the Rossmore Bog in the wetlands on the edge of the Bay of Quinte (Fig. 1) and noted that, in recent years, there had been a change in the bog environment. The authors showed that, at their core site, the forest swamp cover had given way to a later cattail (*Typhea*) swamp and estimated that this change had taken place some 100–150 yr ago.

Examples of high flow or spring flood events (Moira and Trent rivers) have been noted in Fig. 18, and compared with the EI values. There is no consistent relationship between these data. Thus, it does not seem possible to use the Glenora-C core as a means of characterizing individual runoff events, unless of exceptional magnitude. Similarly, it is unlikely that any single cause is responsible for the "noise" in the high-resolution EI data of this core, much of which could be related to the effects of bioturbation (Robbins et al. 1979).

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References

Baumann, P. C., J. F. Kitchell, J. J. Magnuson, and T. B. Kayes. 1974. Lake Wingra, 1837–1973: a case history of human impact. Wisc. Acad. Sci. Arts Lett. 62: 57–94.

Bowlby, J. R. 1975. Late-glacial ice-wedge casts in the Kingston Basin of Lake Ontario. M.Sc. thesis, Department of Geology, Queen's University, Kingston, Ont. 167 p.

Boyce, G. E. 1967. Historic Hastings. Hastings County Council, The Intelligencer, Belleville, Ont. 387 p.

Boyd, C. E. 1970. Production, mineral, accumulation and pigment concentrations in *Typha latifolia* and *Scirpus americanus*. Ecology 51: 285–290.

Bryson, R. A., D. A. Baerreis, and W. M. Wendland. 1970. The character of Late-glacial and Post-glacial climatic changes, p. 53–74. *In* W. Dort Jr. and J. K. Jones Jr. [ed.] Pleistocene and recent environments of the Central Great Plain. Department of Geology, University of Kansas, Spec. Publ. No. 3, Lawrence, KS.

Canniff, W. 1971. The settlement of Upper Canada. Reprinted from the original text published by Dudley and Burns, Toronto, in 1869 by Mika Silk Screening Ltd., Belleville, Ont. 670 p.

Catto, N. R., R. J. Patterson, and W. A. Gorman. 1981. Late Quaternary marine sediments at Chalk River, Ontario. Can. Earth Sci. 18: 1261–1267.

1982. The Late Quaternary geology of the Chalk River region, Ontario and Quebec. Can. J. Earth Sci. 19: 1218–1231.

Chapman, L. J., and D. F. Putnam. 1951. The physiography of southern Ontario. 2nd ed. University of Toronto Press, Toronto, Ont. 386 p.

Christie, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. J. Fish. Res. Board Can. 20: 597–646.

1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

Christie, W. J., and H. A. Regier. 1973. Temperature as a major factor influencing the productive success of fish — two examples. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164: 208–218.

Clark, R. J., and N. P. Persoage. 1970. Some implications of crustal movement in engineering planning. Can. J. Earth Sci. 7: 628–633.

Coleman, A. P. 1937. Lake Iroquois. Ontario Department of Mines, 45th Annual Report, Part VII: 1–36.

CORTS. 1975. The Quinte–Kingston area. Supplementary Report on Optimum Recreation Development in the Quinte–Kingston Area. Canada–Ontario Rideau–Trent–Severn Study Committee. 43 p.

Damiani, V., and R. L. Thomas. 1974. The surficial sediments of the Big Bay section of the Bay of Quinte, Lake Ontario. Can. J. Earth Sci. 11: 1562–1576.

Dreimanis, A., and F. F. Karrow. 1972. Glacial history of the Great Lakes–St. Lawrence region, the classification of the Wisconsinan stage, and its correlatives. 24th Int. Geol. Congr., Montreal, Rep. Sect. 12: 5–15.

Evans, R. D., R. J. Cornett, and V. A. McCulloch 1986. The use of sediments as indicators of point and diffuse source pollution. *In* P. G. Sly [ed.] Sediments and water Interactions. Proc. Third Int. Symp. on interactions between Sediments and Water, Geneva, 1984. Springer-Verlag, New York, NY. (In press)

Fox, M. E., and S. R. Joshi. 1984. The fate of pentachlorophenol in the Bay of Quinte. J. Great Lakes Res. 10: 190–196.

Frank, R., R. L. Thomas, M. V. H. Holdrinet, and V. Damiani. 1980. PCB residues in bottom sediments collected from the Bay of Quinte, Lake Ontario 1972–73. J. Great Lakes Res. 6: 371–376.

Haefeli, C. J. 1972. Groundwater inflow into Lake Ontario from Canadian side. Inland Waters Branch, Department of the Environment, Ottawa, Ont., Sci. Ser. No. 9: 101 p.

Hannon, L. F. 1971. The discoverers. McClelland and Stewart, Toronto, Ont. 256 p.

Hart, J. L. 1980. The spawning and early life history of the whitefish in the Bay of Quinte. Contrib. Can. Biol. Fish. VI (20): 427–444.

Hurley, D. A., and W. J. Christie. 1977. Depreciation of the warm water fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Johnson, M. G., and G. E. Owen. 1970. The role of nutrients and their budgets in the Bay of Quinte, Lake Ontario. Ontario Water Resources Commission Report, August 1970, Toronto, Ont. 28 p.

Johnston, L. M. 1978. Geolimnological studies in the Kingston Basin–Upper St. Lawrence River region Ph.D. thesis, Department of Geology, Queen's University, Kingston, Ont. 243 p.

Kalas, L. L. 1983a. Fluctuation in the Lake Erie fossil mollusc record signifying the changing climate during the past 12,500 years. CCIW unpublished manuscript, Canada Centre for Inland Waters, Burlington, Ont. 22 p.

1983b. Paleo-environmental implications of a mulluscan record in western Lake Erie bottom sediment. CCIW unpublished manuscript, Canada Centre for Inland Waters, Burlington, Ont. 36 p.

Karrow, P. F., T. W. Anderson, A. H. Clarke, L. D. Delorme, and M. R. Sreenivasa. 1975. Stratigraphy, palaeontology, and age of Lake Algonquin sediments in southwestern Ontario, Canada. Q. Res. 5: 49–87.

Karrow, P. F., J. R. Clark, and J. Terasmae. 1961. The age of Lake Iroquois and Lake Ontario. J. Geol. 659–667.

Kay, G. M. 1942. Ottawa–Bonnechere Graben and Lake Ontario homocline. Bull. Geol. Soc. Am. 53: 585–646.

Kemp, A. L. W. 1971. Organic carbon and nitrogen in the surface sediments of Lake Ontario, Erie and Huron. J. Sediment. Petrol. 41: 537–548.

Kemp, A. L. W., C. B. J. Gray and A. Mudrochova. 1972. Changes in C, N, P, and S in the last 140 years in three cores from Lakes Ontario, Erie and Huron, p. 251–279. *In* H. E. Allen and J. R. Kramer [ed.] Nutrients in natural waters. John Wiley & Sons, Inc., New York, NY.

Kemp, A. L. W., R. L. Thomas, H. K. T. Wong, and L. M. Johnston. 1977. Nitrogen and C/N ratios in the sediments of Lake Superior, Huron, St. Clair, Erie, and Ontario. Can. J. Earth Sci. 14: 2402–2413.

Kite, G. W. 1972. An engineering study of crustal movement around the Great Lakes. Inland Water Branch, Department of the Environment, Technical Bulletin 63, Ottawa, Ont. 57 p.

Lamb, H. H. 1977. Climate, past, present and future — climatic history and the future. Vol. 2. Methuen & Co. Ltd., London. 835 p.

Larsen, C. E. 1983. Southern Lake Michigan: evidence for Holocene lake level fluctuations. Unpublished manuscript, U.S. Geol. Survey, Reston, VA. 42 p.

Lehmer, D. J. 1970. Climate and culture history in the Middle Missouri Valley, p. 250–270. *In* W. Dort Jr. and J. K. Jones Jr. [ed.] Pleistocene and recent environments of the Central Great Plains. Department of Geology, University of Kansas, Spec. Publ. No. 3, Lawrence KS.

Lewis, C. F. M. 1969. Late quaternary history of lake levels in the Huron and Erie Basins. Proc. 12th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. 250–270.

Liberty, B. A. 1961a. Belleville and Wellington map-areas, Ontario. Geological Survey of Canada Paper 60-31, Ottawa, Ont. 9 p.

1961b. Rice Lake–Port Hope and Trenton map-areas, Ontario. Geological Survey of Canada Paper 60-14, Ottawa, Ont. 4 p.

1971. Palaeozoic geology of Wolfe Island, Bath, Sydenham and Gananoque map-areas, Ontario. Geological Survey of Canada Paper 70-35, Ottawa, Ont. 12 p.

Lower, A. R. M. 1973. Great Britain's Woodyard. McGill–Queen's University Press, Montreal, Que. 271 p.

Lower Trent Conservation Report. 1970. Ontario Department of Energy and Resources Management, Toronto, Ont. 3 volumes.

Lunn, R., and J. Lunn. 1967. The county. Picton Gazette Publishing Co. Ltd., Picton, Ont. 453 p.

Martin, T. D. 1968. Deseronto and the Rathbun Co. Hastings Historical Society, Belleville, Ont.

Matossian, M. R. 1982. Ergot and the Salem witchcraft affair. Am. Sci. 70: 355–357.

McCombie, A. M. 1967. Some physical and chemical characteristics of the Bay of Quinte. Ontario Department of Lands and Forests Technical Series, Research Report 79, Toronto, Ont. 56 p.

McCrimmon, H. R. 1968. Carp in Canada. Bull. Fish. Res. Board Can. 165: 93 p.

Mika, N., and H. Mika. 1966. Mosaic of Belleville. Mika Silk Screening Ltd., Belleville, Ont. 207 p.

1967. Trenton, past and present. Mika Silk Screening Ltd., Belleville, Ont. 128 p.

1969. Mosaic of Kingston. Mika Silk Screening Ltd., Belleville, Ont. 176 p.

1977. Historic Belleville. Mika Publishing Ltd., Belleville, Ont. 159 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Mirynech, E. 1962. The Pleistocene Geology of the Trenton–Campbellford map-area, Ontario. Ph.D. thesis, Department of Geology, University of Toronto, Toronto, Ont. 240 p.

Moira River Conservation Report. 1950. Ontario Department of Planning and Development, Toronto, Ont. (limited distribution).

Mudroch, A., and J. A. Capobianco. 1979. Effects of mine effluent on uptake of Co, Ni, Cu, As, Zn, Cd, Cr and Pb by aquatic macrophytes. Hydrobiologia 64: 223–231.

1980. Impact of past mining activities on aquatic sediments in Moira River Basin, Ontario. J. Great Lakes Res. 6: 121–128.

Napanee River Conservation Report. 1957. Ontario Department of Planning and Development, Toronto, Ont. (limited distribution).

Ongley, E. D. 1973. Sediment discharge from Canadian basins into Lake Ontario. Can. J. Earth Sci. 10: 146–156.

Ontario Hydro. 1977. A preliminary analysis of the bottom sediments in the vicinity of the proposed submarine cable crossing of Long Reach. Environmental Resources Section, Toronto, Ont. 27 p.

1978. Proposed 230 kV submarine cable — Long Reach, Bay of Quinte. Environmental Resources Section, Toronto, Ont. 23 p.

1980. Analysis of sediments at the shore approaches of the proposed Long Reach submarine cable. Environmental Resources Section, Toronto, Ont. 6 p.

Otto, J. 1983. Sedimentation in the 15, 16, and 20 Mile Creek lagoons and implications for lake level changes, Lake Ontario, p. 85–88. *In* N. A. Rukavina [ed.] Proc. 3rd Workshop on Great Lakes Coastal Erosion and Sedimentation. National Research Council of Canada, Ottawa, Ont.

Payette, S., L. Fillion, L. Gauthier, and Y. Boutin. 1985. Secular climate change in old-growth tree-line vegetation of northern Quebec. Nature (Lond.) 315: 135–138.

PLUARG. 1978. Inventory of land use and land use practices. Vol. V. Canadian Lake Ontario Basin. Pollution from Land Use Activities Reference Group, Task B. International Joint Commission Report 77–023, Windsor, Ont. 85 p.

Prest, V. K. 1970. Quaternary geology of Canada, p. 676–764. *In* R. J. W. Douglas [ed.] Geology and economic minerals of Canada. Geol. Surv. Can. Economic Geology Report 1. 5th ed.

Prince Edward County Conservation Report. 1968. Ontario Department of Energy and Resources Management, Toronto, Ont. (limited distribution).

Prinsenberg, S. J. 1978. Free oscillations in the Lower Bay of Quinte. Manuscript Reports Series No. 7. Research and Development, Ocean and Aquatic Sciences, Canada Centre for Inland Waters, Burlington, Ont. 93 p.

Richards, N. R., and F. F. Morwick. 1948. Soil survey of Prince Edward County. Ontario Soil Survey Report No. 10, Guelph, Ont. 86 p.

Robbins, J. A., P. L. McCall, J. B. Fisher, and J. R. Krezoski. 1979. Effect of deposit feeders on migration of ^{137}Cs in lake sediments. Earth Planet. Sci. Lett. 42: 277–287.

Rukavina, N. A. 1970. Lake Ontario nearshore sediments, Whitby to Wellington, Ontario. Proc. 13th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. 266–273.

Rutherford, G. K. 1972. The clay mineralogy and some properties of bottom sediments of the St. Lawrence River near Kingston, Ontario. Can. J. Earth Sci. 9: 1670–1676.

Scott, W. G., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Sly, P. G. 1983a. Recent sediment stratigraphy and geotechnical characteristics of foreset and bottomset beds of the Niagara Bar. J. Great Lakes Res. 9: 224–233.

1983b. Sedimentology and geochemistry of recent sediments off the mouth of the Niagara River, Lake Ontario. J. Great Lakes Res. 9: 134–159.

1984. Sedimentology and geochemistry of modern sediments in the Kingston basin of Lake Ontario. J. Great Lakes Res. 10: 358–374.

Sly, P. G., and J. W. Prior. 1984. Lake-glacial and post-glacial geology of Lake Ontario. Can. J. Earth Sci. 21: 802–821.

Starling, R. N. 1978. Modern pollen in the Salmon River Basin. Ph.D. thesis, Department of Biology, Queen's University, Kingston, Ont. 464 p.

Stommel, H., and E. Stommel. 1979. The year without a summer. Sci. Am. 240(6): 176–186.

Terasmae, J. 1980. Some problems of late-Wisconsin history and geochronology in southeastern Ontario. Can. J. Earth. Sci. 17: 361–381.

Terasmae, J., and E. Mirynech. 1964. Post-glacial chronology and the origin of deep lake basins in Prince Edward County, Ontario. Publ. II, Great Lakes Res. Div., Univ. Michigan, Ann Arbor, MI. p 161–169.

Thomas, M. K. 1968. Some notes on the climatic history of the Great Lakes region. Proc. Entomol. Soc. Ont. 99: 21–31.

Thomas, R. L., A. L. W. Kemp, and C. F. M. Lewis. 1972. Distribution, composition and characteristics of the surficial sediments of Lake Ontario. J. Sedment. Petrol. 42: 66–84.

Warwick, W. F. 1978. Man and the Bay of Quinte, Lake Ontario: 2800 years of cultural influence, with special reference to the chironomidae (Diptera), sedimentation and eutrophication. Ph.D. thesis, University of Manitoba, Winnipeg, Man. 290 p.

Wright, J. V. 1972. Ontario pre-history. National Museum of Man, Ottawa, Ont. 120 p.

Exchange Flows in the Adolphus Reach/North Channel

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Freeman, N. G., and S. J. Prinsenberg. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Current meter observations taken in the summers of 1976 and 1978 in the interconnecting gaps of the Adolphus Reach/North Channel basin are used to explain the dominant exchange flows with Lake Ontario and the upper Bay of Quinte. Histograms of current meter records from two years indicate the persistence of a clockwise circulation around Amherst Island and a two-layer estuarine-type flow through the Glenora Gap. Wind-induced currents lasting for 3–5 d represent a major mechanism for flushing the North Channel. Spectral analysis of current meter data and the application of the Defant method for barotropic and baroclinic free oscillations in partially enclosed basins show that the most energetic oscillatory motion is the 5.2-h co-oscillation of the Adolphus Reach/North Channel basin with Lake Ontario through Collins Bay Gap. A two-layered channel model successfully predicts along-stream and cross-stream thermocline slopes and entrainment velocities for the exchange flow at Glenora Gap.

On se sert d'observations faites à l'aide de courantomètres à l'été de 1976 et de 1978 dans les brèches reliées entre elles du bassin du chenal North et du chenal Adolphus pour expliquer les échanges dominants avec le lac Ontario et la partie supérieure de la baie de Quinte. Les histogrammes des données enregistrées par les courantomètres pendant deux ans montrent la persistance d'une circulation se faisant dans le sens des aiguilles d'une montre autour de l'île Amherst et d'un écoulement de type estuarien en deux couches passant par la brèche de Glenora. Les courants dus aux vents, d'une durée variant de trois à cinq jours, constituent un mécanisme important de lessivage du chenal North. L'analyse spectrale des données fournies par les courantomètres et l'application de la méthode de Defant pour les oscillations libres barotropiques et baroclinques dans des bassins à demi enfermés montrent que le mouvement d'oscillation le plus énergétique est la cooscillation de 5,2 h du bassin du chenal North et du chenal Adolphus avec le lac Ontario par la brèche de la baie Collins. Un modèle de chenal en deux couches prédit avec succès les gradients thermiques et les vitesses d'entraînement le long et en travers des cours d'eau pour les échanges qui se font au niveau de la brèche de Glenora.

Introduction

The Bay of Quinte is located at the northeastern corner of Lake Ontario and connects the Trent River canal system with the lake. The subject of this study is the lower portion of the Bay of Quinte called Adolphus Reach and North Channel (Fig. 1). This partially enclosed basin is approximately 44 km long from Picton Bay in the southwest to Collins Bay in the northeast, with an average depth of 28 m and an average width of 2 km. Water mass exchange with Lake Ontario takes place through two gaps: Upper Gap and the gap off Collins Bay (designated Collins Bay Gap), with sill depths of approximately 24 m. Exchange with the upper Bay of Quinte takes place through the narrower and shallower (18 m) gap at Glenora (designated Glenora Gap). Water movements occur in the Adolphus Reach/North Channel basin in response to wind stress applied at the free surface, internal and surface forces applied at the gaps by motions in Lake Ontario and the upper Bay of Quinte, and internal pressure fields caused by differential heating and thermocline depression.

Current measurements in the Adolphus Reach/North Channel basin were begun in the summer of 1976 to provide some preliminary information on the water mass exchange processes with Lake Ontario and with the upper Bay of Quinte. This information was needed to help explain biological observations ongoing in "Project Quinte" and to provide the background for assessing possible changes in exchange between the Bay of Quinte and Lake Ontario brought about by the hypolimnetic extraction and surface return of the recently installed thermoelectric generating station at Lennox. A second field program was carried out in the spring of 1978 to provide considerably more detail on the two-layer exchange flow at the Glenora Gap, in particular, the seasonal variability from early May to late October.

In this paper the observational data base is examined to ascertain the various scales of motion through the interconnecting gaps, including barotropic, baroclinic, long-term, episodal, and oscillatory. The cause and effect relationships are hypothesized by examining related wind, water level, and temperature data. Using the 1976 current meter data, bulk flow estimates are computed for each of the gaps at different flow scales. Next, theoretical barotropic and baroclinic free oscillation periods are calculated and compared with the spectrally analyzed current meter data. And finally, a two-layered theoretical model for flow through straits is used for making entrainment estimates and force balances in the Glenora Gap.

Materials and Methods

Single mooring strings, containing two Plessey current meters at depths of 7 and 22 m, were scheduled for each of the Upper, Glenora, and Collins Bay gaps for the period June 10 to

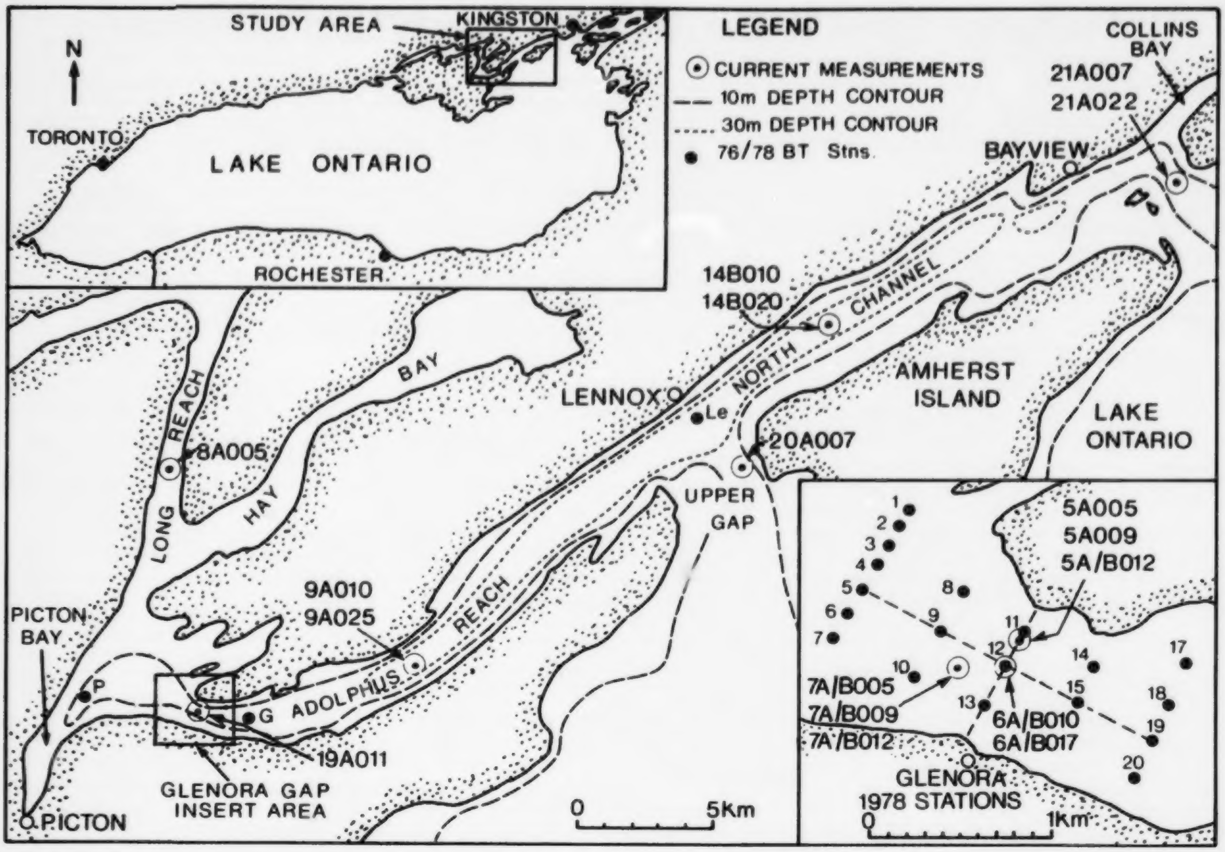

STUDY AREA
KINGSTON
N
TORONTO
LAKE ONTARIO
ROCHESTER
LEGEND
CURRENT MEASUREMENTS
10m DEPTH CONTOUR
30m DEPTH CONTOUR
76/78 BT Stns.
COLLINS BAY
21A007
21A022
BAYVIEW
14B010
14B020
NORTH CHANNEL
AMHERST ISLAND
LAKE ONTARIO
LENNOX
Le
20A007
UPPER GAP
LONG REACH
BAY
HAY
8A005
9A010
9A025
ADOLPHUS REACH
PICTON BAY
P
G
19A011
GLENORA GAP INSERT AREA
PICTON
0
5Km
5A005
5A009
5A/B012
7A/B005
7A/B009
7A/B012
6A/B010
6A/B017
GLENORA
1978 STATIONS
0
1Km
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
17
18
19
20

FIG. 1. Locations of current meter moorings and bathythermograph stations for 1976 and 1978. The first two digits of the current meter number give the mooring location, the alpha character the deployment period, and the last two digits the rounded-off value of the instrument depth in metres. Moorings 19, 20, and 21 are from 1976, while the rest are from 1978.

October 27, 1976. However, due to a predeployment instrument failure, only one meter was available for the Glenora mooring, and it was deployed at 11 m depth. Owing to a malfunctioning compass, the record from the bottom meter on the Upper Gap mooring was also unusable. These current meter locations are shown in Fig. 1. In addition to fixed mooring records, weekly profiles of temperature were made during the summer of 1976 at three locations (stations P, G, and Le in Fig. 1) to obtain an estimate of the seasonal variation in the thermal structure.

The first current meter deployment in 1978 took place on May 4, with three moorings in the Glenora Gap. The two outside moorings (5 and 7) each contained a Plessey current meter at 4.5 m depth and two Geodynes at 8.5 and 11.5 m. The central mooring consisted of two Geodyne current meters located at 10 and 17 m depth. In addition to the Glenora moorings, a single Geodyne current meter was placed at 4.5 m depth in the southern portion of Long Reach. The final two Geodyne current meters deployed on May 4 were at station 9, approximately 8 km east of the Glenora Gap, at depths of 10 and 25 m.

On July 11, 1978, these current meters were retrieved and the three Glenora Gap moorings refurbished and redeployed in the same location. The station 9 mooring was moved to station 14 in the North Channel with the Geodyne current meters placed at 10 and 20 m depths. This second mooring deployment ran for a period of approximately 3 mo with all meters recovered on October 14, 1978.

Approximately weekly throughout the summer of 1978, temperature profiles were collected at 20 stations in Glenora Gap (Fig. 1, inset). In addition, a series of vertical current profiles, using a hand-lowered Endeco current meter, were taken at the three moored current meter stations. Temperature sections and vertical current profiles for June 22, 1978, are discussed in this paper.

The 10-min data from the Geodyne current meters and the 20-min data from the Plessey current meters were filtered and decimated to half-hourly values before the auto- and cross-spectra were run. A complete and usable data set was obtained from the four current meters deployed in 1976 and from all the current meters scheduled and installed in the first deployment in 1978; however, current meters 5B005 and 5B009 produced a nil record and 7B005 only a partial record (1 mo) on the second deployment. It should be noted that both winds and currents are plotted as flow towards, rather than flow from. Directions are measured clockwise in degrees relative to true north and the current vectors as *u* (east) and *v* (north).

Discussion of Observations

In examining the 1976 and 1978 time-series data for the Adolphus Reach/North Channel basin, three distinct time scales seem to emerge: (1) the long-term or prevailing flows which are relatively uniform over periods of a month and appear to be driven by the discharge of the Trent River; (2) the episodal flows which seem to be coupled directly and sometimes indirectly to

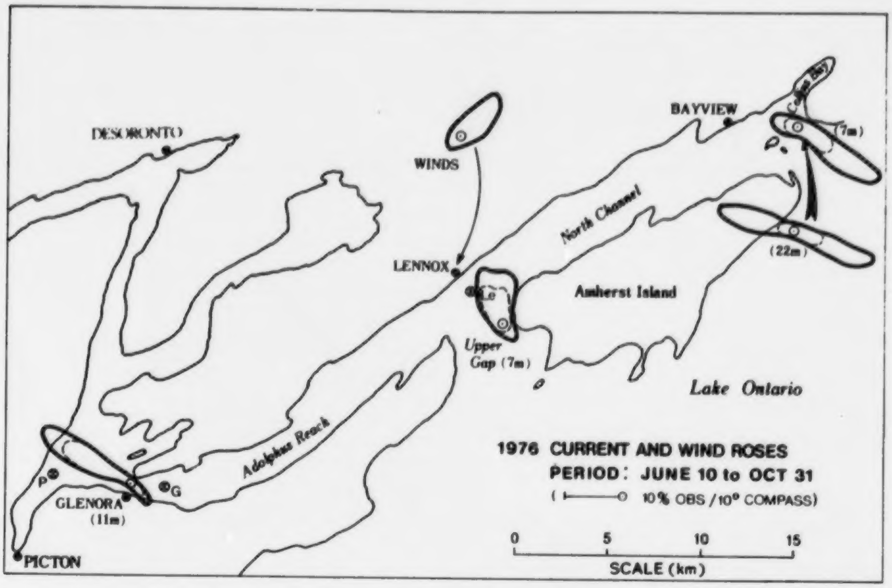


FIG. 2. Current and wind roses for the 1976 data set. The distance of the solid line from the centre point (circle) indicates the percentage of speed observations that fall within a 10° compass interval; the broken line provides the same information, but for speeds less than 10 cm/s.

TABLE 1. Estimates of mean currents U (cm/s) and transports Q (m^3/s) for different averaging periods of the 1976 current data.

		Glenora Gap			Upper Gap			Collins Bay Gap			
			Lower layer			Upper layer		Upper layer		Lower layer	
Type of flow	Period	h_1 (m)	U	Q	h_1 (m)	U	Q	U	Q	U	Q
Long-term two-layer flow	June 20 – July 30	7	−5.5	−484	10	+0.7	+63	−2.0	−200	−0.1	−14
	Aug. 10 – Sept. 20	15	−2.6[a]	NA	15	+0.7	+95	−2.8	−420	+2.9	+261
One-layer flow	Sept. 26 – Oct. 26	H	+0.4	+58	H	+3.1	+669	−3.6	−732[b]	−2.5	NA
Short-term two-layer flow	July 17–19.5	8	−5.0	−400	10	−10.1	−909	−12.8	−1280	+20.6	+2884
	July 27–28.5	9	−3.0	−216	17	−13.0	−1989	−4.0	−680	+20.6	+1442
	Sept. 4–5.5	13	+5.0[a]	+520	20	−8.5	−1530	+11.7	+2340	+18.7	+748
Short-term one-layer flow	Oct. 8–9	H	+1.5	+216	H	+15.8	+3476	−18.4	−4356	−17.9	NA
	Oct. 22–23.5	H	−2.7	−378	H	−6.4	−1408	+12.2	+3672	+18.4	NA
	Oct. 25–26	H	+1.5	+210	H	+11.7	+2574	−17.0	−4296	−18.8	NA
Mean depth (h) (m)		18			24			24			
Mean breadth (b) (km)		0.8			0.9			1.0			
Mean cross-sectional area (m^2)		1.4×10^4			2.2×10^4			2.4×10^4			

NOTE: H = water column homogeneous; − = out of Adolphus Reach/North Channel basin; + = into Adolphus Reach/North Channel basin; NA = not applicable. Total basin means: h = 36.5 m; b = 2.0 km; L = 34.0 km; volume = 2.48×10^9 m^3.

[a] Current meter possibly in upper layer.

[b] Lower and upper layer velocities averaged.

2- and 3-d weather systems passing over the area; and (3) the oscillatory flows of a few hours duration which are linked to the free oscillations of the Adolphus Reach/ North Channel basin.

Long-Term Flows

To examine the long-term flows, current roses are developed for each current meter record using all the observations for the full period of deployment. Current and wind roses for the 1976 observations are given in Fig.2; mean currents, averaged over different time periods, are given in Table 1. The broken lines on the roses in both Fig. 2 and 3 indicate the percentage of currents whose speed falls below 10 cm/s. The area between the broken and solid lines represents the percentage of currents over 10 cm/s. As can be observed, the most frequent speeds are generally less than 10 cm/s except at Collins Bay Gap where speeds in excess of this predominate. It is interesting to note that the prevailing surface flow (at least at 7 m depth) is into the

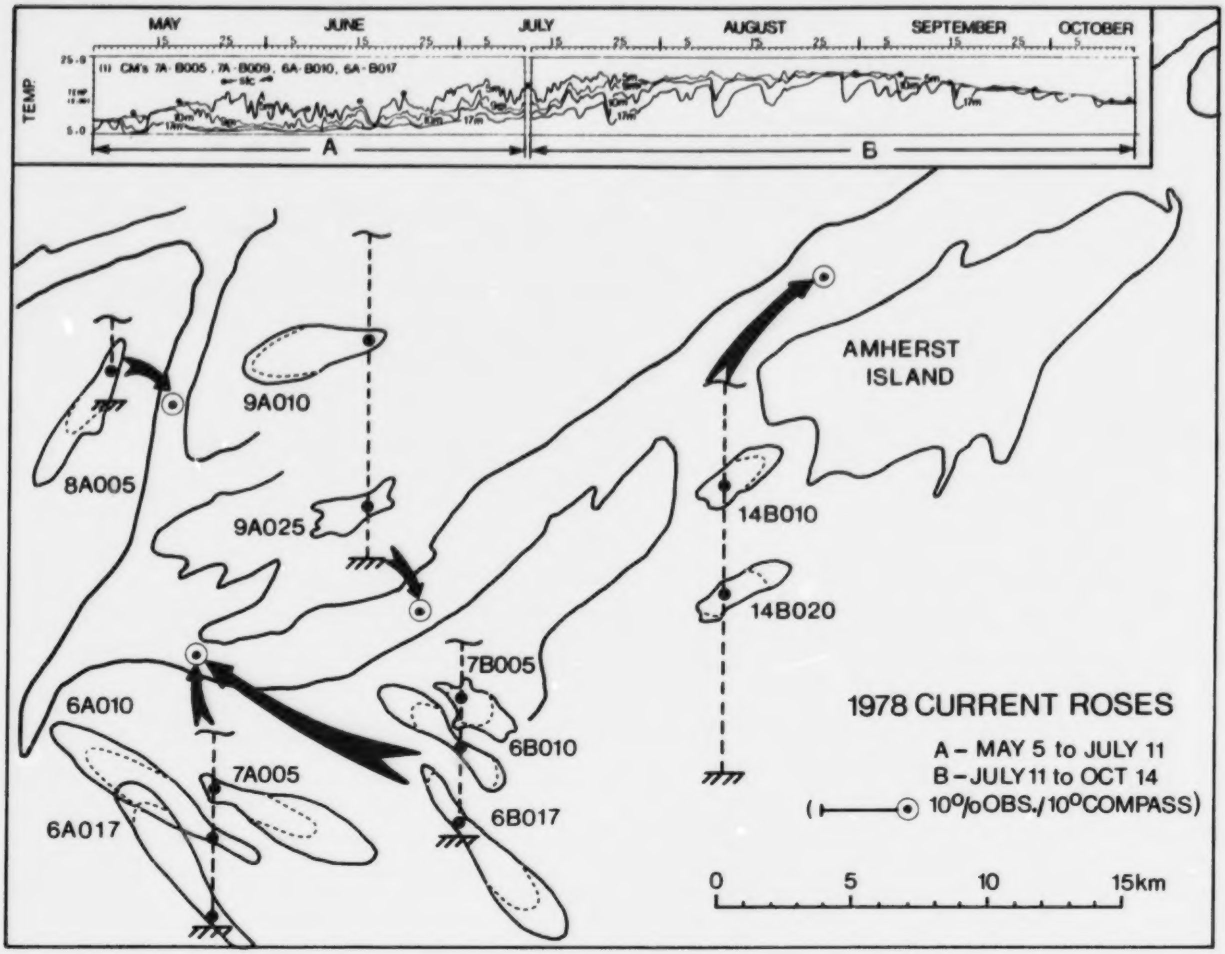


FIG. 3. Current roses for the 1978 data set. There are two different periods of record and the current roses are placed at their appropriate scaled depth in the water column (vertical broken lines; wave indicates surface). The inset gives a time-series record of water temperature at various depths in the Glenora Gap for the two periods of record.

North Channel through the Upper Gap and out through the Collins Bay Gap, thus creating a general clockwise circulation around Amherst Island. At Glenora the most significant feature of the prevailing flow at 11 m depth is that it is from Adolphus Reach into Long Reach and not out as would be expected from a strictly barotropic consideration of the river discharge. Thus, a prevailing bidirectional exchange flow must exist between Long Reach and Adolphus reach.

A two-layered exchange flow process through Glenora Gap is evident in the current roses for the 1978 current meter records presented in Fig. 3. For the first deployment period (A, May 5 to July 11, 1978) there is a substantial river discharge from the Trent River, particularly during the month of May, as reflected in the prevailing southward flow in the Long Reach record 8A005. In the Glenora Gap, the flow at 4.5 m is almost exclusively from Long Reach into Adolphus Reach, with a substantial return flow evident at 10 and 17 m depth. It should be noted that the surface current meter record 7A005 contains twice as many observations of speeds greater than 10 cm/s as either of the lower two meters 6A010 or 6A017. Roses from current meters 9A010 and 9A025, approximately 8 km to the east in Adolphus Reach, show prevailing currents to the west at both the 10 and 25 m depths. This is consistent with the prevailing two-layer circulation observed at Glenora in the first deployment period.

During the second deployment (B, July 11 to October 14, 1978) the surface flow through Glenora Gap into Adolphus Reach is significantly reduced due to an order of magnitude reduction in river discharge. From mid-August onward there appears to be a significant flow reversal in the two-layer circulation. The 10 m depth record 6B010, which is now well above the seasonal thermocline, indicates a prevailing flow out of Adolphus Reach, and the 17 m record 6B017 indicates a prevailing flow into the Reach. This is because the seasonal thermocline in the Adolphus Reach/North Channel basin (see Fig. 9) is below the sill depth at Glenora and the thermocline now slopes downward reversing the density-driven flows in the upper and lower layers. From mid-September to mid-October the flow is uniform from surface to bottom as the water column becomes more homogeneous through cooling of the surface layers. This is reflected in the 40% inflow at 10 m depth (6B010) and part of the much larger inflow at 17 m depth (6B017).

Current meters (14B010, 14B020) were also installed in the North Channel during the second deployment period. They indicate a prevailing northeasterly flow at both 10 and 20 m depth, confirming the long-term clockwise circulation around Amherst Island indicated in the 1976 current meter records.

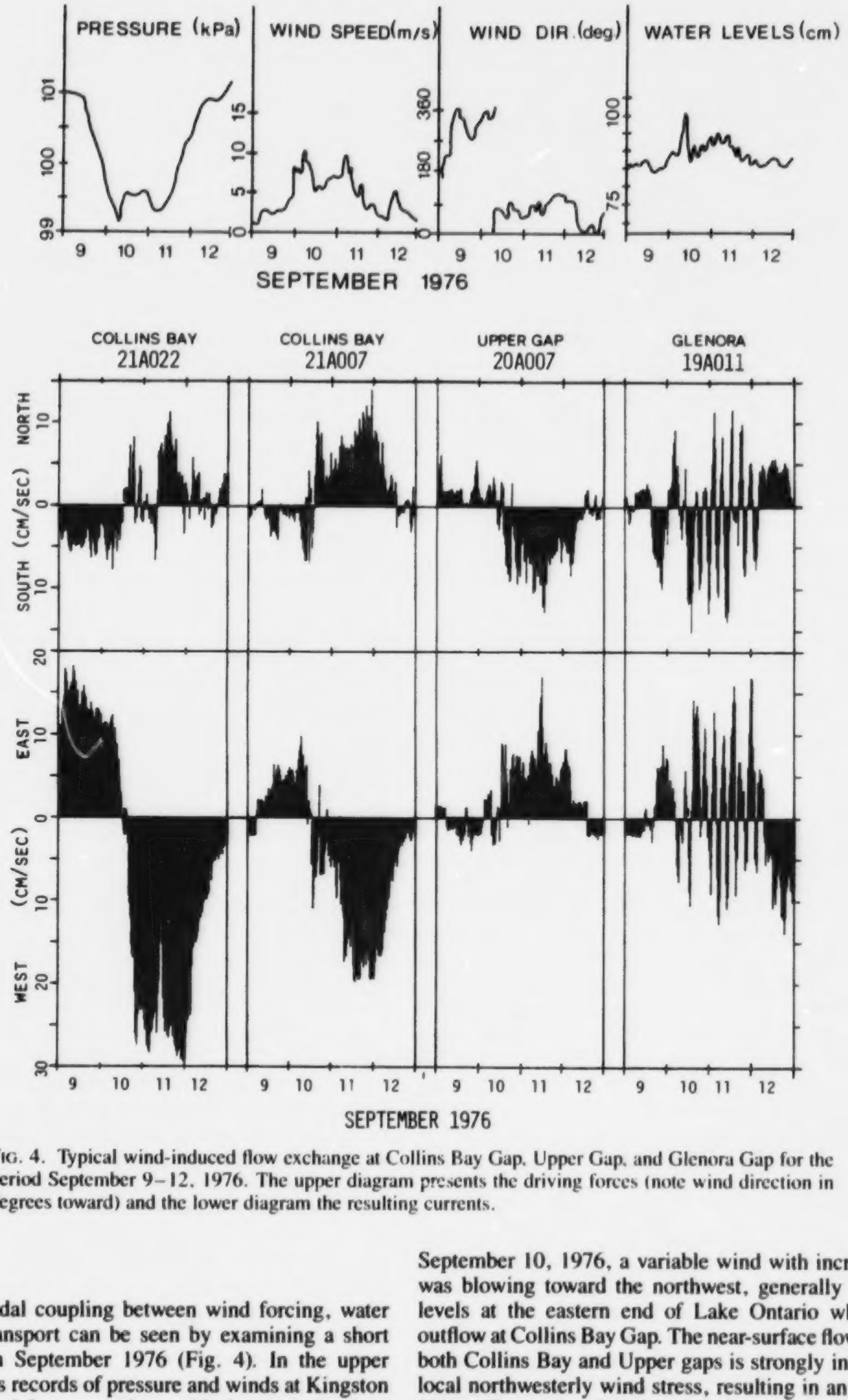


FIG. 4. Typical wind-induced flow exchange at Collins Bay Gap, Upper Gap, and Glenora Gap for the period September 9–12, 1976. The upper diagram presents the driving forces (note wind direction in degrees toward) and the lower diagram the resulting currents.

Episodal Flows

The strong episodal coupling between wind forcing, water level, and water transport can be seen by examining a short period of record in September 1976 (Fig. 4). In the upper diagram, time-series records of pressure and winds at Kingston Airport are presented for comparison with the water levels at Kingston Harbour, and in the lower diagram the corresponding currents in the interconnecting gaps of the Adolphus Reach/North Channel basin are given. This series of wind episodes is very similar to the August 9, 1972, storm simulated by Simons (1975). Winds blowing toward the northwest lowered water levels at the eastern end of Lake Ontario, while winds blowing toward the east over Lake Ontario raised them. Prior to 06:00 on September 10, 1976, a variable wind with increasing strength was blowing toward the northwest, generally lowering water levels at the eastern end of Lake Ontario which caused an outflow at Collins Bay Gap. The near-surface flow (7 m depth) in both Collins Bay and Upper gaps is strongly influenced by the local northwesterly wind stress, resulting in an inflow through Upper Gap and a diminished surface outflow through Collins Bay Gap. However, with the passage of the low pressure system a steady and much stronger wind toward the east–northeast developed, causing a sudden rise in water level at the eastern end of Lake Ontario and flow reversals in the Collins Bay and Upper gaps. The hydraulic head between Lake Ontario and the North Channel is responsible for driving a barotropic flow into the North Channel over the entire depth; however, in the surface

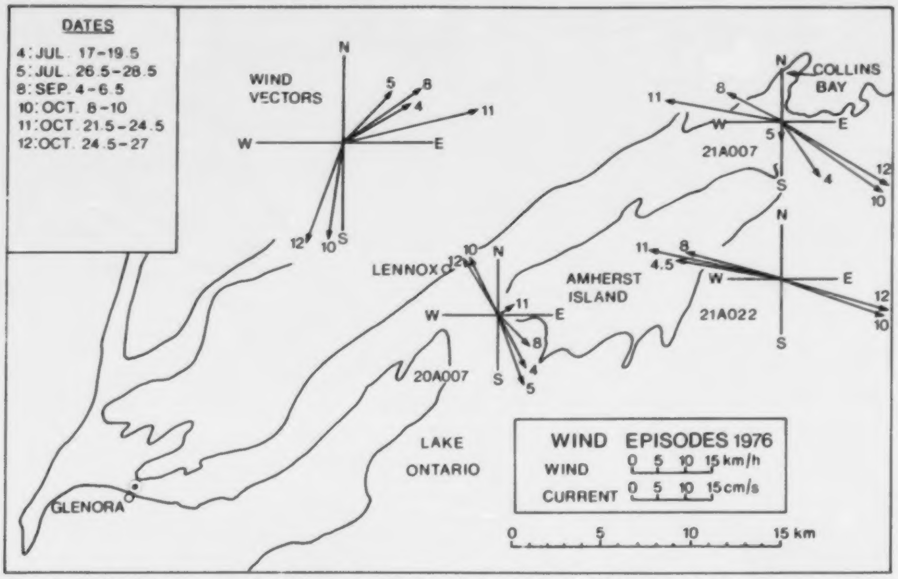


FIG. 5. Episodal current and wind vectors for six steady wind periods between July and October 1976. Both wind and current are plotted as direction toward, with the length of the vector indicating the speed.

layer (7 m depth) the direct wind forcing opposes this hydraulically driven inflow, with the result that surface water is forced out of Upper Gap and the surface inflow in Collins Bay Gap is somewhat decreased. Through Glenora Gap there is a strong oscillatory motion with the same 5-h period seen in the Kingston water level record. This oscillation shows up in the Glenora current meter record due to the strong flow convergence through Glenora Gap and results from the quarter wave resonance of the Adolphus Reach/North Channel basin with Lake Ontario as forced through Collins Bay Gap. A small net surface flow into Adolphus Reach is due principally to wind stress on the water resident in the Glenora Gap.

Twelve episodal events were isolated from the 1976 current meter time-series records and analyzed as to their direct coupling with winds at Lennox. Only episodes that had steady wind forcing prior to and during the episode were chosen. Current vectors and corresponding wind vectors for six representative episodes are plotted in Fig. 5. In the majority of the cases, winds as recorded at Lennox were blowing toward the northeast along the axis of the embayment. These winds generally produced inflow at the surface (7 m) and at depth (22 m) in Collins Bay Gap and outflow at the surface (7 m) at Upper Gap. The two predominant storms in the fall (10 and 12), in which the winds blew toward the south–southwest, caused a reversal in the flow exchange. Thus, winds toward the northeast normally cause an anticlockwise circulation around Amherst Island and winds toward the south–southwest induce a clockwise circulation. Generally, direct wind forcing appears to produce an anticlockwise circulation that opposes the hydraulically driven long-term clockwise circulation around Amherst Island.

Oscillatory Flows

Oscillatory motions can be seen in the water level record for Kingston and the current meter record at Glenora (Fig. 4). These periodic motions are related to the fundamental free oscillations of Adolphus Reach/North Channel and Lake Ontario basins.

Figure 6 presents autospectra of the principal current components for the three surface current meters. Basically, three periodic regimes can be observed: (1) 5.2 h which is associated with the fundamental free oscillation of Lake Ontario (Hamblin and Rodgers 1967) and 2.3 h with the first mode of the Adolphus Reach/North Channel basin; (2) semidiurnal periods (see also Hamblin 1968) related to tidal flows and semidiurnal east–west winds; and (3) the longer periods of 60 and 140 h associated with the passage of weather systems or internal motions in the Adolphus Reach/North Channel basin.

In Fig. 6, significant peaks appear at 5.2, 3.2, and 1.4 h in the spectra for Glenora Gap and at 2.3 and 1.4 h for Upper and Collins Bay gaps. The first mode of Lake Ontario (5.2 h) is amplified in Glenora Gap, absent in Upper Gap, and present but not significantly in Collins Bay Gap. Similarly, a peak at the semidiurnal period occurs in the spectra at both ends of the basin but appears attenuated in the middle location (Upper Gap). The 2.3 and 1.4 peaks are present in all spectra and as seen later are associated with east–west barotropic oscillations within the basin itself. Peaks at larger periods lack spatial (horizontal) coherence, suggesting independent motions at the ends of the basin at these periods. These periods are usually associated with baroclinic oscillations whose periods vary throughout the season as the vertical temperature structure varies.

Using the more extensive current records collected in 1978 in the Glenora Gap, cross-spectra were run to examine the horizontal and vertical coherence of the exchange flow through this particular gap. As can be seen in the upper diagram of Fig. 7, the horizontal coherence is most significant for the 5.2- and 90-h periods. The phase relationship at these periods is close to zero, indicating that on the horizontal scale of kilometres, the water moves as a coherent mass.

For the vertical coherence shown in the lower diagram of Fig. 7, the 5.2- and 90-h periods are still the most coherent; however, in this case the longer period motions are definitely 180° out of phase. This would confirm the long-term two-layer (baroclinic) flow exchange in which currents in the upper layer flow in opposite direction to currents in the lower layer. It is interesting to note that at 5.2 h the currents in the upper and lower layers are in phase (that is, both flowing in the same direction), confirming the barotropic nature of the high-

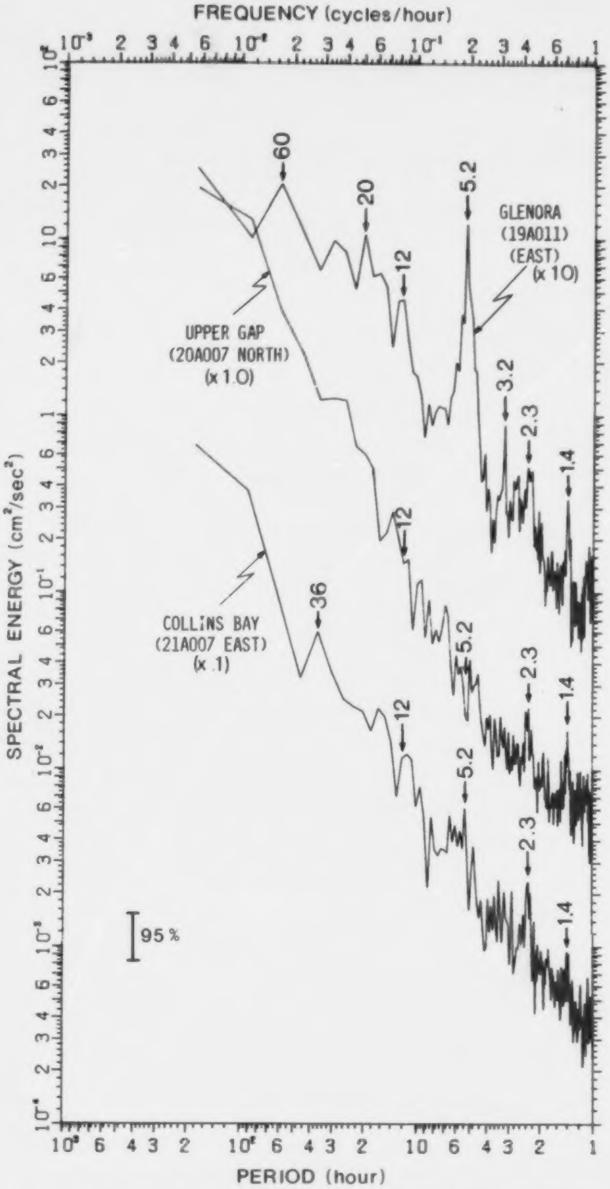


FIG. 6. Autospectra of current meter records for the period June 10– by an order of October 31, 1976. Note that the scales are staggered magnitude to enable presentation of all three records on the same graph.

frequency basin oscillations.

Bulk Flow Computations

The four 1976 current meter records were used to obtain order of magnitude estimates of the bulk flows through the gaps to provide typical values for nutrient and chemical budget calculations. The averaging period is just over 1 mo for the long-term flows and 2–3 d for the short-term exchanges. During the summer period, transport through the gap is calculated only for the layer in which the current meter was then located. As given in Table 1, typical values range from 10 to 4000 m³/s, the discharge of a small stream all the way up the mighty St. Lawrence River. An estimate of the accuracy of such bulk flow computations can be made during the relatively homogeneous period from September 26 to October 26, 1976. During this period the Trent River discharge, the major river flowing into the Bay of Quinte upstream of the Glenora Gap, averaged about 68 m³/s and is comparable with the Glenora Gap average inflow of 58 m³/s (Table 1). This inflow is balanced by a net outflow at the eastern end of North Channel of 63 m³/s through Collins Bay Gap. The computations in Table 1, however, represent only order of magnitude flow estimates, as there was no opportunity to assess the cross-channel variations in the flow fields.

From these estimates some representative bulk flushing periods can be computed. For example, the June 20 to July 30 long-term lower layer transport at Glenora of −484 m³/s would indicate that the bottom 26 m of the Adolphus Reach/North Channel basin would be completely flushed within 43 d. During the fall (say October 8–9, 1976), the transport at Collins Bay Gap of −4356 m³/s would be sufficient to drain the entire North Channel within 3 d. Finally, it should be pointed out that all the episodal and most of the steady transports are generally an order of magnitude larger than the 62.5 m³/s discharge from the Lennox generating station.

Theoretical Basin Oscillations

Surface and internal oscillations within a bay or lake can be greatly affected by the natural resonance conditions of the area itself. For certain outside periodic disturbances, a bay or lake acts as a resonator and magnifies the amplitudes of the resulting long-period waves above those which one would expect. The periods that the basin will amplify out of a broad band of available wave periods are called the natural periods of oscillation and depend on the topographic features of the area, the boundary conditions, and the vertical density structure.

Two-Layered Basin Model

Areas with a strong vertical density stratification can experience large internal wave oscillations which show up in horizontal current meter data but not in the surface elevation data. The governing equations for a two-layered vertical density structure of a lake or bay with variable depth and width are as follows for the lower layer (Proudman 1952):

$$(1)\qquad \frac{\partial(u_2 h_2 b)}{\partial x} + b\left(\frac{\partial \eta_2}{\partial t}\right) = 0$$

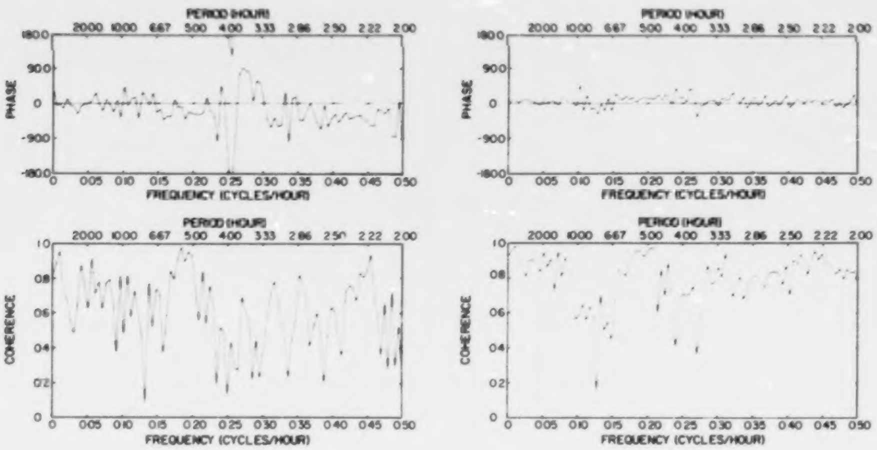
$$(2)\qquad \frac{\partial u_2}{\partial t} = -g'\left(\frac{h_1}{h_1 + h_2}\right)\frac{\partial \eta_2}{\partial x}$$

where u_2, h_2, and ρ_2 are the lower layer velocity, thickness, and density, b is the channel width, h_1 and ρ_1 are the upper layer thickness and density, η_2 is the interface displacement, and g' is the "reduced" gravity constant given by

$$(3)\qquad g' = g\left(\frac{\rho_2 - \rho_1}{\rho_2}\right).$$

Equations (1) and (2) are thus similar to those used by Defant's (1961) method for the surface mode. Actually, the transformation of the two-layer equations to equivalent one-layer equations is only valid if the lower layer depth is constant. Mortimer (1979) noted that errors arising from variable cross-section areas are below 10% as long as the lower depth does not change too abruptly between sections as is the case for the Adolphus Reach/North Channel basin. Thus, the theoretical baroclinic free oscillation periods of the Adolphus Reach/North Channel basin were obtained by Defant's iterative method using equations (1), (2), and (3). To obtain the barotropic free oscilla-

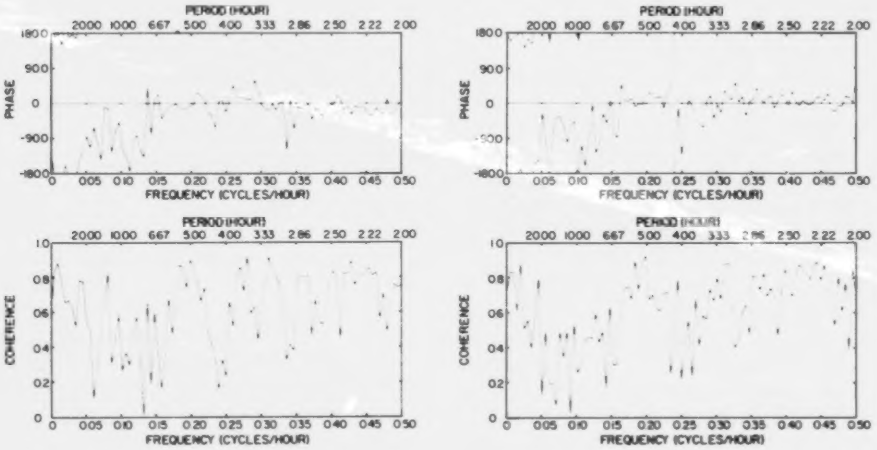
a) HORIZONTAL COHERENCE



5A005 Vs 7A005

5B012 Vs 6B010

b) VERTICAL COHERENCE



5A005 Vs 5A012

7A005 Vs 6A017

FIG. 7. Coherence and phase spectra for different combinations of current meter records (1978): (a) May 5 – July 11; (b) July 11 – October 14. In each case only the *u* (east) component of velocity is used for the cross-spectral estimates.

tion periods the same equations and numerical scheme were used but η_2 was replaced by the free-surface displacement, h_2 by the total basin depth, u_2 by the total velocity, and $g'h_1(h_1 + h_2)^{-1}$ by the gravitational constant. The 44-km-long region, as indicated in the upper diagram of Fig. 8, was divided into 20 sections of equal 2.2-km lengths and Defant's method applied using the average depth and width for each section.

Computed Barotropic Closed Basin Periods

The surface or barotropic periods for a closed basin were computed using a starting surface displacement of 100 cm at the southwestern end of the region (see Prinsenberg 1978). The corresponding surface elevations and horizontal velocities for the first three surface modes are given in Fig. 8b. The resulting periods are 1.4 h for the first mode, 0.8 h for the second mode, and 0.5 h for the third mode. The largest values in surface elevation and horizontal currents for the region are predicted for the section at Glenora where the small cross-sectional area magnifies the surface wave properties. The model predicts that the longitudinal currents at Glenora and Bayview are in phase for the first modal period of 1.4 h and the third modal period of 0.5 h, whereas they are out of phase for the second modal period of 0.8 h. The ratio of current energy (2.5) for Glenora Gap relative to Upper Gap (Fig. 8b) computed from the model compares well with the observed value of 2.1 (Fig. 6). The theoretical ratio of energy for the Bayview location relative to the Upper Gap is 0.02 and also compares well with the observed value of 0.6 considering that the current at Bayview is forced to zero in the model (Fig. 8).

Computed Barotropic Open Basin Periods

Open bay modes can also be calculated by Defant's method.

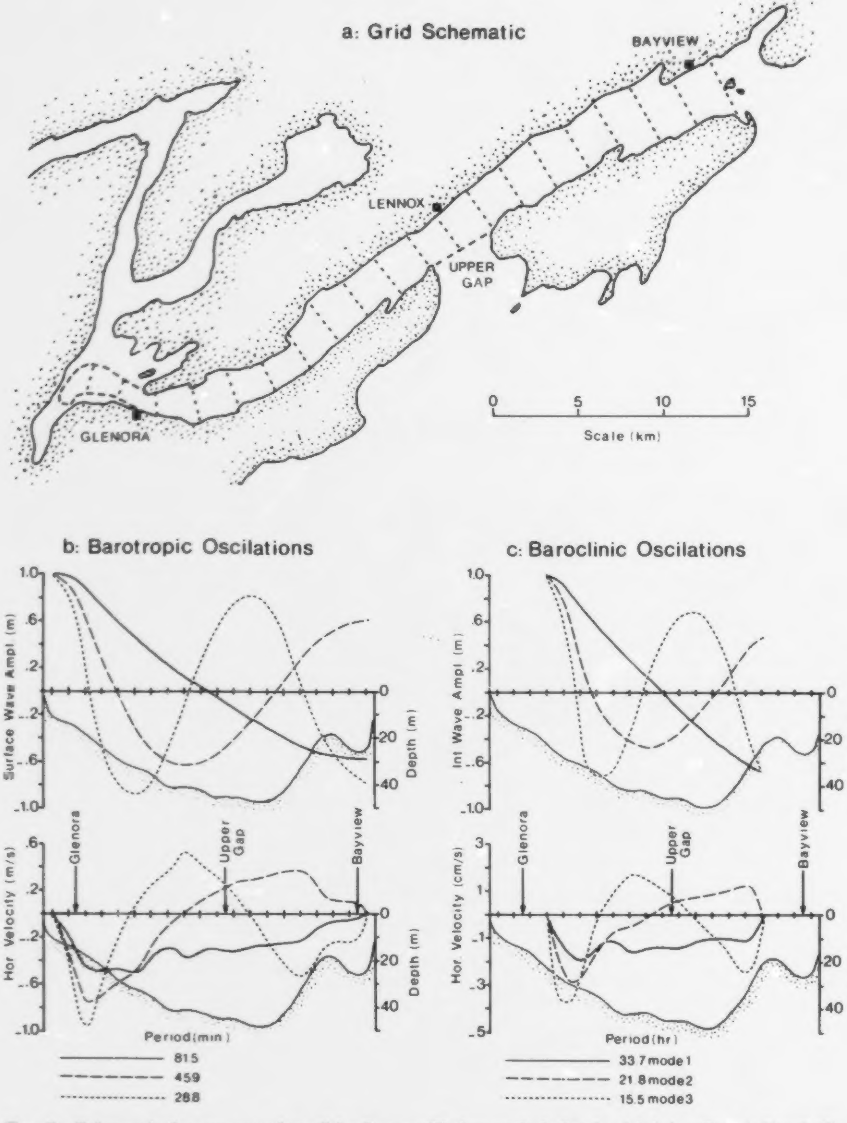


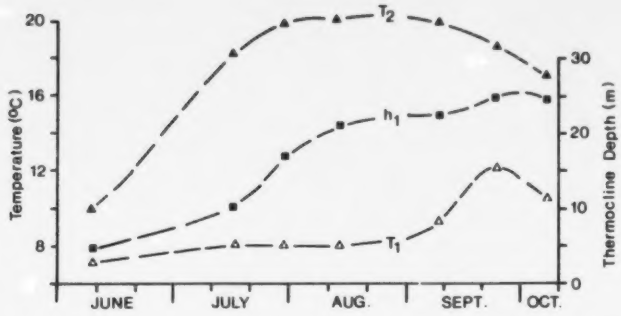
FIG. 8. Schematic for computation of the free oscillation periods for the Adolphus Reach/North Channel basin. The lower diagrams give the computed surface and interface displacements as well as the velocity distributions along the principal axis of the basin for the first three modes of the barotropic and baroclinical basin oscillations. A thermocline depth of 21 m and normalized density difference of 1.64×10^{-3} were used for the baroclinic computations (c).

The two connecting channels between the Adolphus Reach/North Channel basin and Lake Ontario both have 24 m sill depths and can admit energy into the region for possible resonance. No new modal periods for either the surface mode or internal mode are obtained when the periodic energy disturbance enters the area by means of Upper Gap, as it is located at an antinode of the Adolphus Reach/North Channel basin. When energy enters the region through the northern passage, however, the complete length of the region is available for co-oscillation at an odd multiple of quarter wave lengths. The surface modal resonant periods for the open boundary case are 2.7 h for the first mode, 1.1 h for the second mode, and 0.7 h for the third mode.

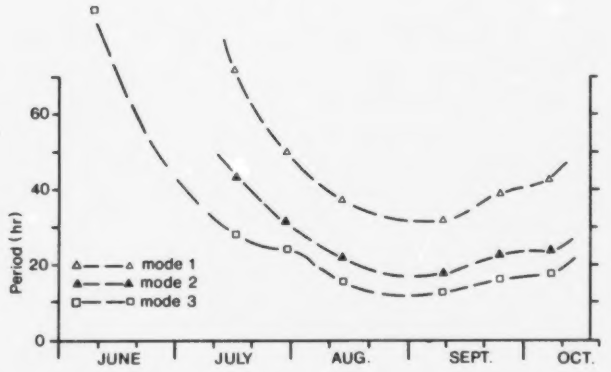
It should be noted that the autospectra presented in Fig. 6 confirm the existence of significant periodicities at both the closed and open basin fundamental free oscillation periods, 1.4 and 2.3 h, respectively. It appears that the Adolphus Reach/North Channel basin co-oscillates with Lake Ontario through Collins Bay Gap at nearly the open bay resonant period of 2.7 h. Theory shows that the water level is amplified at the western end of the basin (Glenora) and strong water level and current oscillations occur there. Simultaneous water level records (June 1978) from Kingston and Glenora show strong correlation at this period.

Computed Baroclinic Closed Basin Periods

The resonant periods for the internal modes of the Adolphus Reach/North Channel basin vary throughout the summer in

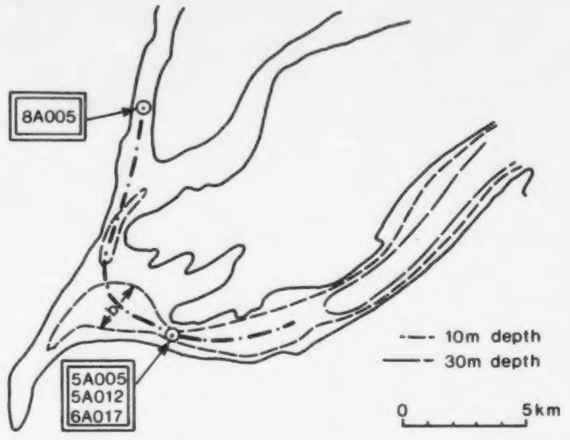


a) INPUT PARAMETERS

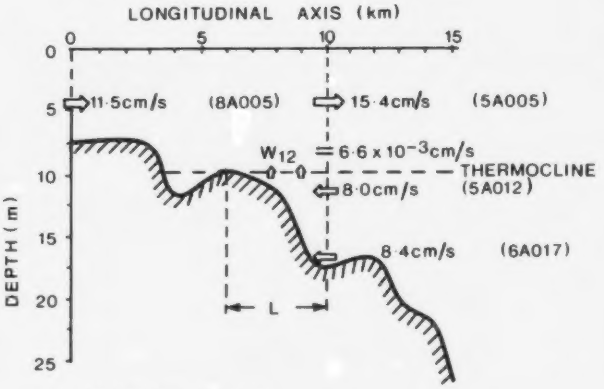


b) COMPUTED BAROCLINIC PERIODS

FIG. 9. (a) Seasonal variation in the thermocline depth and the surface and bottom layer temperatures; (b) computed baroclinic free oscillation periods from June to October 1976 using these input parameters.



a) Horizontal Section



b) Vertical Section

FIG. 10. Schematic for the computation of an entrainment velocity in the Glenora section for a uniform river discharge period of May 19–22, 1978. The average currents for this period are given in the lower diagram at the appropriate current meter depth.

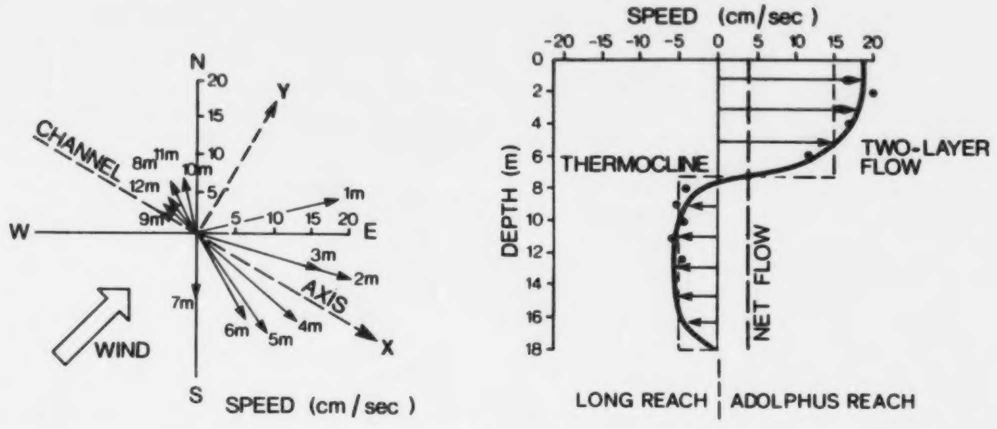
response to the changing thermocline depth and density structure of the water column. The thermocline depth actually becomes deeper than some of the average depths of the cross-sections, thus shortening the length of the basin for internal wave resonance relative to the length for surface wave resonance. Figure 8c shows the results of the Defant method for an average summer case with a thermocline depth of 21.0 m, and a water temperature change from 20°C in the upper layer to 8°C in the lower layer. The periods found by the model are 37.7 h for the first mode, 21.8 h for the second mode, and 15.5 h for the third mode. It should be noted that both the amplitudes and resulting velocities are relative to the amplitude specified at the Glenora end.

The summer variation of the thermocline depths and temperature values for the upper and lower layer in the vicinity of the Lennox Generating Station is shown in Fig. 9a (Ontario Hydro 1974). The corresponding variation in the value of the baroclinic resonance period of the first three internal modes are shown in Fig. 9b. In the spring, a shallow and weak thermocline is present which results in long modal periods. As the thermocline deepens and the temperature difference between the layers increases, the internal modal periods decrease to average summer values. The fall cooling and associated surface layer overturning starts in early September. This phenomenon decreases the temperature difference between the layers but increases the thermocline depth. The effects on modal period offset each other and the average summer period values extend into the month of September before increasing to infinity when the whole water column overturns and becomes homogeneous. The modal periods appear to be nearly constant over the period covering the last 3 wk of August and the month of September.

Spectra of sections of the total current record (Prinsenberg 1978) showed that statistically significant energy peaks occurred at longer periods but varied in position moving to shorter periods in midsummer. This was predicted by the model for the internal modes. The major long period peak moved from 60 h in the spring to 20 h in the summer and fall. Both also show up as significant peaks in the total Glenora record (Fig. 6) and are thought to be associated with the first internal resonance mode whose period decreased during the observation period as shown in Fig. 9. These energy peaks do not show up in the other records of Fig. 6, as the current meters are actually outside the sills separating the basin and Lake Ontario.

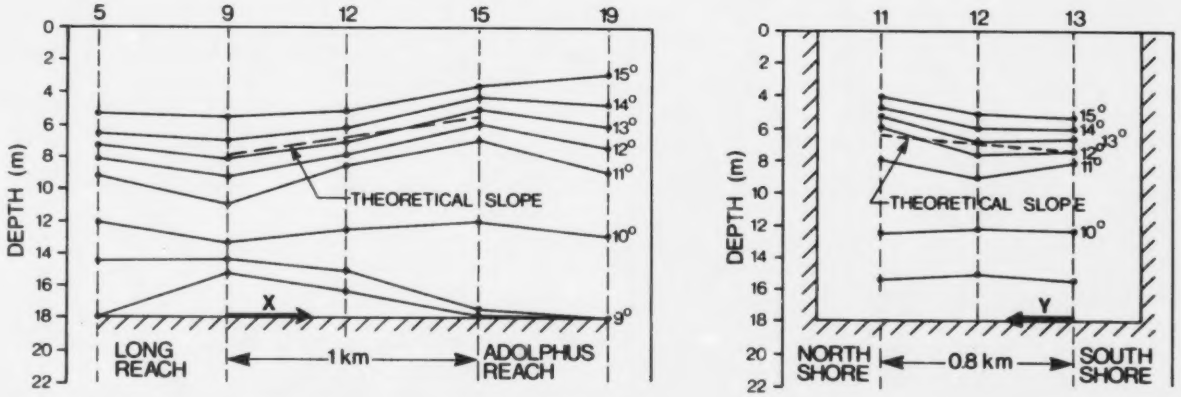
Theoretical Channel Flows

The exchange flow at the Glenora Gap is examined in more detail using classical concepts of vertical entrainment and two-layer channel flow. Two sets of observations (May 19–22, 1978, and June 22, 1978) are used as input and verification of these simplified models.



(a) CURRENT VECTORS

(b) VERTICAL CURRENT PROFILE



(c) LONGITUDINAL TEMPERATURE CONTOURS

(d) TRANSVERSE TEMP. CONTOURS

FIG. 11. Current vectors, temperature profiles, and contours for the 1-day intensive field observational program in the Glenora Gap on June 22, 1978. The theoretically calculated curves are superimposed on the observed data.

Entrainment Computations

The vertical section from station 8A on Long Reach to station 5A in the Glenora Gap is considered as a classical two-layer estuary (Fig. 10). Conservation of mass can then be applied to this control volume to estimate the mean vertical entrainment velocity. The river discharge, mainly from the Trent River, can be estimated from the current observations of meter 8A005 and verified against the measured Trent River discharge (designated as $u_0 h_0 b_0$). The outflow from the upper layer is represented by $u_1 h_1 b_1$ and is computed from current meter 5A005. The return flow in the bottom layer, $u_2 h_2 b_2$, can be calculated by averaging the two current meters 5A012 and 6A017. The water mass and heat balance for the total control volume then becomes

$$(4) \quad u_1 h_1 b_1 - u_0 h_0 b_0 = u_2 h_2 b_2$$

$$(5) \quad T_1 u_1 h_1 b_1 - T_0 u_0 h_0 b_0 = T_2 u_2 h_2 b_2$$

where h_0 and b_0 are the depth and width at the upstream station, $(h_1 + h_2)$ and b_1 are the depth and width at the downstream location, and h_1 is the depth of the thermocline. The continuity of mass for the lower control volume gives the value for entrainment velocity w_{12} from the lower layer to the top layer:

$$(6) \quad w_{12} L b = u_2 h_2 b_2$$

where L and b are defined in Fig. 10. The entrainment coefficient is defined as

$$(7) \quad E = 2w_{12}/(u_0 + u_1).$$

From May 19 to 22, 1978, the Trent River was in maximum flood (as given by daily discharge data, Water Survey of Canada), and flow through the Glenora Gap was persistent and uniform over this period. The currents indicated in Fig. 10b represent average flows over this period of time. The following values were used for computations in equations (4), (5), (6), and (7). $u_0 = 11.5$ cm/s, $u_1 = 15.4$ cm/s, $u_2 = 8.2$ cm/s, $L = 4 \times 10^5$ cm, $h_0 = 750$ cm, $h_1 = 1000$ cm, $h_2 = 800$ cm, $T_0 = 18$°C, $T_1 = 13$°C, $T_2 = 6$°C, $b_0 = 0.8 \times 10^5$ cm, $b_1 = 0.8 \times 10^5$ cm, $b_2 = 0.8 \times 10^5$ cm, and $b = 2.0 \times 10^5$ cm. From equations 4 and 5 a value of 15.2 cm/s was computed for u_1 and a value of 12.6°C for T_1, which compare well with the observed values given above. The values for entrainment velocity and coefficient are $w_{12} = 6.6 \times 10^{-3}$ cm/s and $E = 5 \times 10^{-4}$. These values are consistent with estuarine entrainment values (Cordes et al. 1980).

Longitudinal Balance of Forces

To learn more about the driving mechanisms for this two-layered flow, a longitudinal balance of forces can be coupled with actual field observations to make an estimate of the longitudinal slope of the interface as shown in Fig. 11c. A steady wind of about 15 mph from the southwest persisted throughout the day of June 22, 1978. This wind stress was responsible for moving warm surface water from the southern regions of Long Reach towards the western end of Glenora Gap, depressing the thermocline and driving the two-layer exchange flow, shown in Fig. 11b, through the gap. Direct wind stress in the first few metres diverts the flow in the wind direction (Fig. 11a).

Using the vertically integrated two-layer equations of motion derived by Freeman (1982), the along-channel (x-direction) momentum balance is expressed for the upper and lower layers, respectively, as

$$(8) \qquad g\frac{\partial \eta_1}{\partial x} = -\frac{\tau_{ix}}{\rho_1 h_1}$$

$$(9) \qquad g'\frac{\partial \eta_2}{\partial x} = -g\frac{\partial \eta_1}{\partial x} + \left(\frac{\tau_{ix} - \tau_{bx}}{\rho_2 h_2}\right)$$

where η_1 and η_2 are the free surface and interface displacements, τ_{ix} and τ_{bx} the interface and bottom shear stresses, h_1 and h_2 are the thickness of the upper and lower layer, and the assumptions of steady-state, no along-channel wind stress, and no cross-channel vertically averaged velocity have been made. Combining equations (8) and (9) and substituting in quadratic shear stress laws, an expression that balances the interface slope against the interface and bottom shear stresses is obtained:

$$(10) \qquad \frac{\partial \eta_2}{\partial x} = \frac{1}{g'}\left(k_i\left(\frac{h_1 + h_2}{h_1 h_2}\right)(u_1 - u_2)|u_1 - u_2| - \frac{k_b}{h_2}u_2|u_2|\right).$$

The following physical parameter values taken from Fig. 11b and friction coefficients (k_i, k_b) taken from Dick and Marsalek (1972) are used to calculate the internal slope at Glenora: u_1 = 15 cm/s, u_2 = -5 cm/s, h_1 = 7 m, h_2 = 11 m, $g \simeq 10^3$ cm/s^2, $(\rho_2 - \rho_1)/\rho_2$ = 0.00065, k_b = 0.002, and k_i = 0.0014. Substituting these values into equation (10), an interface slope of 2.1×10^{-3} is obtained, which means that over 1 km the interface height will increase by 2.1 m. This line is plotted on the actual measured temperature contours (Fig. 11c) and its slope aligns very well with the slope of the observed thermocline. It is also interesting to note that the dominant terms in the above computation are the balance of the lower layer pressure gradient and the interfacial shear stress.

Cross-Channel Balance of Forces

Additional evidence of the existence of this two-layered flow exchange between Long Reach and Adolphus Reach can be obtained by examining the cross-channel geostrophic, wind stress, and interfacial slope balance. With the y-axis across the channel (running from southwest to northeast), the cross-channel momentum balance for the two layers is

$$(11) \qquad g\frac{\partial \eta_1}{\partial y} = -fu_1 + \frac{\tau_{sy}}{\rho_1 h_1}$$

$$(12) \qquad g\frac{\partial \eta_1}{\partial y} + g'\frac{\partial \eta_2}{\partial y} = -fu_2$$

where f is the coriolis parameter, τ_{sy} is the surface wind stress, and the assumptions of steady-state and negligible interface and bottom stresses (i.e. much less than the wind stress) have been made. Substituting equation (11) into equation (12), the following expression for the interface slope is obtained:

$$(13) \qquad \frac{\partial \eta_2}{\partial y} = \frac{1}{g'}\left[f(u_2 - u_1) - \frac{\rho_a k|V_a|V_a}{\rho_1 h_1}\right]$$

where ρ_a is the air density, k is the wind stress coefficient, and V_a is the cross-channel wind speed. Using the same numerical values as in the previous example and choosing a wind stress coefficient of 1.85×10^{-3} (Simons 1981) and $f = 10^{-4}$/s, the numerical value for the interface slope is 0.91×10^{-3}. Thus, over the 0.8-km channel breadth the interface slope will increase by 0.7 m from the south shore to the north shore. This theoretical slope estimate is plotted on Fig. 11d and agrees well with the observed temperature field. It is interesting to note that the Coriolis term is only slightly larger than the cross-channel wind stress but is in the opposite direction.

Conclusions

During the summer the bottom flow generally appears to be decoupled from the surface flow (baroclinic processes), while during the fall the two are strongly coupled (barotropic processes). A long-term clockwise circulation exists around Amherst Island, consistent with a hydraulic head across Collins Bay Gap, due to seasonal lowering of Lake Ontario. Prevailing flow at depth in Glenora Gap is into the upper Bay of Quinte and indicates the existence of a long-term two-layered exchange flow. Direct wind coupling associated with the passage of weather systems causes water mass exchange episodes on the order of 3–5 d, which represents a major mechanism for flushing of the Adolphus Reach/North Channel basin, particularly the North Channel.

By far the most energetic oscillatory motion is at the Glenora Gap and is caused by the 5.2-h co-oscillation of the Adolphus Reach/North Channel basin through the Collins Bay Gap with the fundamental free oscillation of Lake Ontario. Long-term bulk flow estimates show that the flushing of the hypolimnion of the Bay of Quinte through the Glenora Gap would take 43 d, while an episode of 2–3 d in the fall can completely flush the North Channel through Collins Bay Gap. All the episodal, and most of the steady transports, are an order of magnitude larger than the discharge from the Lennox Generating Station. In any event, the hypolimnetic water extracted by Lennox will be replaced by two-layered flow exchange with Lake Ontario.

The Defant method for computation of baroclinic oscillations in a partially enclosed basin can be extended to the computation of internal seiche modes. The baroclinic periods, particularly the quarter wavelength open bay periods (2.7 h, 1.1 h, etc.), agree well with the observed periods from the spectral analysis of current meter data. The barotropic periods (on the order of 15–70 h) as determined by the model, are difficult to verify, due to variation of the internal wave period from spring to summer.

A simple steady-state two-layered channel flow model, in which wind stress is balanced by surface slopes and shear stresses, was successfully tested against the Glenora 1978 current and bathythermograph data. A water mass balance at the Glenora Gap gave vertical entrainment coefficient velocities on the order of 7×10^{-3} cm/s and entrainment coefficient of 5×10^{-4}.

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References

Cordes, R. E., S. Pond, B. R. de Lange Boom, P. H. LeBlond, and P. B. Crean. 1980. Estimates of entrainment in the Fraser River plume, British Columbia. Atmosphere-Ocean, 18(1): 15–26.

Defant, A. 1961. Physical oceanography. Vol. 2. The Macmillan Company, New York, NY. 598 p.

Dick, T. M., and J. Marsalek. 1972. Thermal wedge between Lake Ontario and Hamilton Harbour. Proceedings of the 15th Conference on Great Lakes Research. p. 536–543.

Freeman, N. G. 1982. Measurement and modelling of freshwater plumes under an ice cover. Ph.D. thesis, University of Waterloo, Waterloo, Ont. 152 p.

Hamblin, P. F. 1968. The variation of the water level in the western end of Lake Ontario. Proceedings of the 11th Conference on Great Lakes Research. p. 385–397.

Hamblin, P. F., and G. K. Rodgers. 1967. Currents in the Toronto region of Lake Ontario. Great Lakes Institute, PR29, University of Toronto, Toronto, Ont.

Mortimer, C. H. 1979. Strategies for coupling data collections and analysis with dynamic modelling of lake motions, p. 183–222. *In* Graft, Wit, and C. H. Mortimer [ed.] Lake hydrodynamics. Elsevier, Devel. Water Sci. II, Amsterdam, The Netherlands.

Ontario Hydro. 1974. Lake Ontario water temperatures in the vicinity of Lennox Generating Station 1971–1973. Hydraulic Investigations Section, Ontario Hydro.

Prinsenberg, S. J. 1978. Free oscillations in the lower Bay of Quinte. Manuscript Report Series No. 7, Ocean and Aquatic Sciences, Central Region, Environment Canada. 93 p. (Unpublished manuscript)

Proudman, J. 1952.Dynamic oceanography. Dover Publications Inc., New York, NY. 409 p.

Simons, T. J. 1975. Verification of numerical models of Lake Ontario. II. Stratified circulations and temperature changes. J. Phys. Oceanogr. 5(1): 98–110.

1981. Circulation models of lakes and inland seas. Can. Bull. Fish. Aquat. Sci. 203: 146 p.

Temperature and Oxygen Conditions and Oxygen Depletion in the Bay of Quinte, Lake Ontario

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The summer temperature and oxygen regimes thoughout the Bay of Quinte between 1972 and 1983 are described. Oxygen depletion rates at stations in the lower Bay are calculated and analysed. The link between oxygen depletion and eutrophication is examined. Oxygen depletion did not respond to decreased point-source phosphorus loading. There was little evidence of change of trophic state in the lower Bay, and oxygen depletion rates were consistent. Oxygen depletion rates were not related to hypolimnetic temperature or warming rates.

On décrit les régimes estivaux de la température et de l'oxygène dans la baie de Quinte pour la période 1972–1983. Les taux d'appauvrissement en oxygène à des stations situées dans la partie inférieure de la baie sont calculés et analysés. Le lien entre l'appauvrissement en oxygène et l'eutrophisation est examiné : le premier n'a pas réagi à une charge locale diminuée en phosphore. Il n'y avait que de faibles signes d'un changement de l'état trophique dans la partie inférieure de la baie ; les taux d'appauvrissement en oxygène concordaient. Ces derniers n'étaient pas liés à la température hypolimnique ou aux taux de réchauffement.

Introduction

The link between hypolimnetic oxygen depletion (HOD) and eutrophication (or productivity) in lakes has been much studied (Hutchinson 1957; Vollenweider and Janus 1982). Regression models constructed with data from a range of lakes, such as Charlton (1980) and Cornett and Rigler (1979), predict that decreases in phosphorus loading should produce reductions in hypolimnetic oxygen depletion rates.

After decades of increasing nutrient loading to the Bay of Quinte (Minns 1986a), there was concern in the late 1960's that the hypolimnion of Adolphus Reach (Fig. 1) might go anoxic. Comparison of then current data (McCombie 1967) with that of Tucker (1948) showed a decrease in late summer of hypolimnetic oxygen levels at the Conway station (C). During the course of Project Quinte (1972 to present), we monitored temperature and oxygen conditions at a number of stations throughout the Bay. The immediate objectives were to measure (i) the year-to-year changes and spatial differences in conditions and (ii) bottom oxygen depletion rates at those stations where the waters stratify in summer. Given the then available models, our null hypothesis was that HOD rates in the middle and lower Bay would decrease in response to large reductions (60–70%, Minns et al. 1986) in point-source phosphorus loading, beginning in 1978.

A complicating factor was the climate-forced exchange flows between Adolphus Reach and the outlet basin of Lake Ontario, discovered by Freeman and Prinsenberg (1986). These flows undermine stratification and as a result the hypolimnion warms considerably over the summer. Near Glenora (GL), where the mixing forces are greatest because of channel narrowing, upwelling occurs. Charlton (1980) has shown how HOD rates are determined by lake productivity, i.e. nutrient inputs, temperature, and the volume of the hypolimnion. In large deep lakes, it is expected that hypolimnia will remain cool throughout the summer and that the large volume can accommodate oxygen demand below the thermocline. Given the mixing in Adolphus Reach, our second null hypothesis was that warming would increase oxygen depletion rates.

Materials and Methods

The temperature and oxygen measurements were made at a number of stations, usually weekly from May to September (Fig. 1). Most temperature profiles were determined using a Hydrographic telethermometer (model FT3), which was calibrated against a standard centigrade thermometer (0.5°C accuracy). Sometimes, a Van Dorn sampler was used to bring water to the surface and temperatures were measured by placing the probe into the sampler. Most oxygen profiles were measured using a Y.S.I. model 54 dissolved oxygen meter and self-stirring probe on samples drawn with a Van Dorn sampler, although early measurements were made using a Winkler's titration. Calibration was usually determined against air-saturated distilled water. Accuracy was estimated to be ±0.2 $mg \cdot L^{-1}$. Most recently, a Y.S.I. model 54 dissolved oxygen meter with a submersible probe was used to record both temperature and oxygen profiles. At shallow stations (15 m), temperature and oxygen were generally measured at 1-m intervals. At deeper stations, profiles were generally measured at 2-m intervals, but sometimes at 1 or 5 m. Measurements were nearly always made within 1 m of the bottom. Besides the main station data, other data sets were available. D. A. Hurley (Glenora Fisheries Station, pers. comm.) had monitored a number of sites

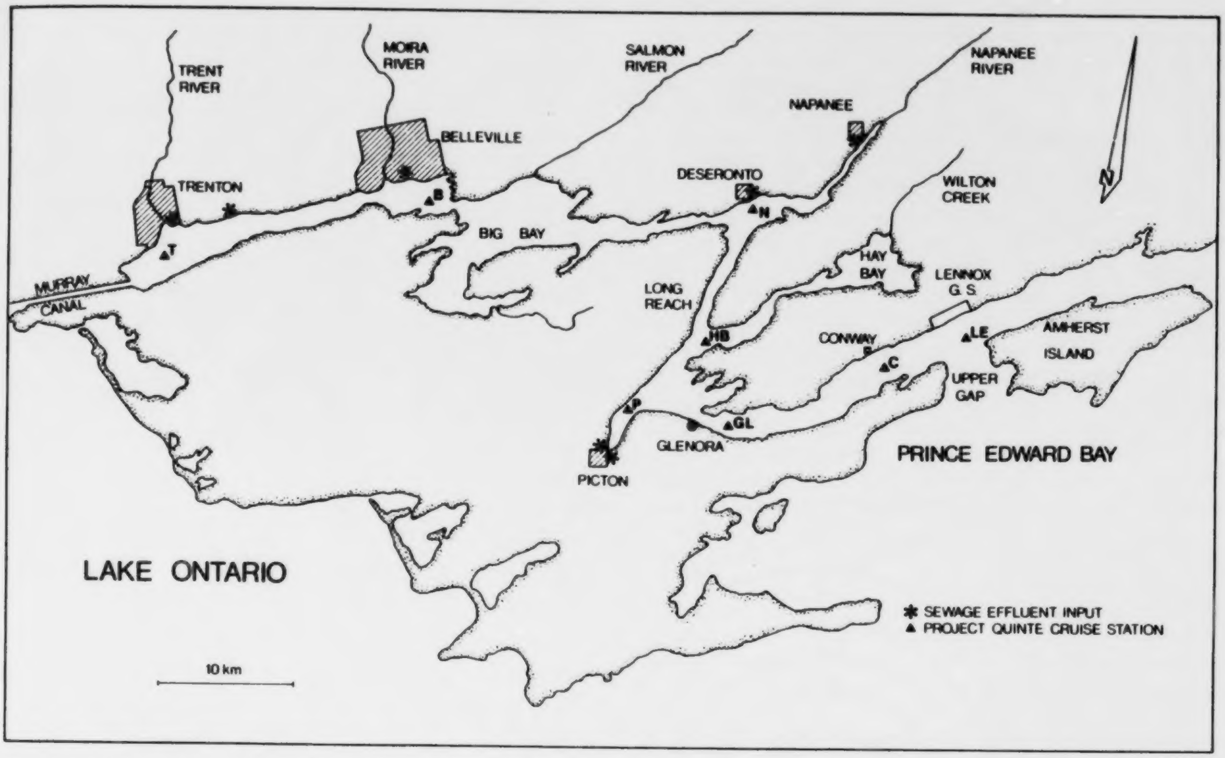

FIG. 1. Location of the main sampling stations in the Bay of Quinte.

throughout the Bay at monthly intervals from May to October from 1967 to 1983. M. G. Johnson had unpublished data for Big Bay, Glenora, and Conway for the period 1967–69. The Ontario Ministry of the Environment had data on file for a number of stations from 1967 to 1979. In addition, in 1975–77, an extensive grid of stations in Adolphus Reach was monitored weekly in the summer in conjunction with a survey of *Pontoporeia* distribution (Johnson and McNeil 1986). The majority of statistical analyses were carried out using the SPSS package as implemented on a CDC Cyber.

Besides the general data file containing all temperature and oxygen measurement records, a subfile was created for some analyses consisting of surface and near bottom values by station, date, and year. Values were selected according to following:

(i) Surface values: nearest to the surface between the depths zero and Z_c.

(ii) Bottom values: nearest the bottom (Z_m) between the depths ($Z_m - Z_c$) and Z_m.

(iii) Critical depth (Z_c) equals $5/3 + Z_m/15$.

This procedure is systematic but arbitrary. At a station of depth 5 m, surface values would only be drawn between 0 and 2 m and bottom values between 3 and 5 m. At a 50-m station, the comparable values are 0–5 m and 45–50 m.

Results

Seasonal and Spatial Trends, 1972–83

The seasonal and spatial patterns are consistent as shown by the results obtained for surface and bottom waters at Belleville (B), Hay Bay (HB), and Conway (C) (Fig. 1) between 1972 and 1983 (Fig. 2).

At Belleville (station depth $\simeq$5 m), there is no stratification. Each year a warming trend continues into June (Fig. 2a), followed by a plateau which lasts until the end of August with some peaks over 25°C. At Hay Bay (station depth $\simeq$11 m) and Conway (station depth $\simeq$30 m), there is stratification, beginning near the end of April, and oxygen depletion occurs (Fig. 2b, 2c). At Hay Bay, oxygen levels often decline to low levels, $\simeq 1.0\ \mathrm{mg \cdot L^{-1}}$, in August but the epilimnion eventually obliterates the hypolimnion and anoxia never occurs. At Conway, there is a steady warming of the hypolimnion and bottom oxygen levels decline to $2-4\ \mathrm{mg \cdot L^{-1}}$ before turnover occurs in late September or early October.

A percentage frequency tabulation of all data by temperature and percentage oxygen saturation ranges shows that there was a high occurrence of supersaturation ranging from 40.7% in region 1 to 27.3% in region 4 (Table 1). This is consistent with the high levels of primary production occurring in the surface waters of the Bay (Millard and Johnson 1986). Saturation levels less than 60% were most prevalent in the Picton–Hay Bay area, 11.2%, and in Adolphus Reach, 14.6%, where oxygen depletion occurred.

In Adolphus Reach, stratification generally becomes evident at the end of June, e.g. Conway, 1977 and 1980 (Fig. 3a, 3b). The thermocline, as represented by the 15°C isotherm, continues to deepen throughout the summer although there may be marked vertical displacements likely due to seiches and storms. In 1977 (Fig. 3a), the summer was marked by a series of warming and cooling periods. Vertical stratification in the lower Bay is not nearly as sharp as might be expected in a lake of comparable size (Hutchinson 1957).

Oxygen levels at Conway remain uniform until the middle or end of July (Fig. 3a, 3b) when some depletion of oxygen is

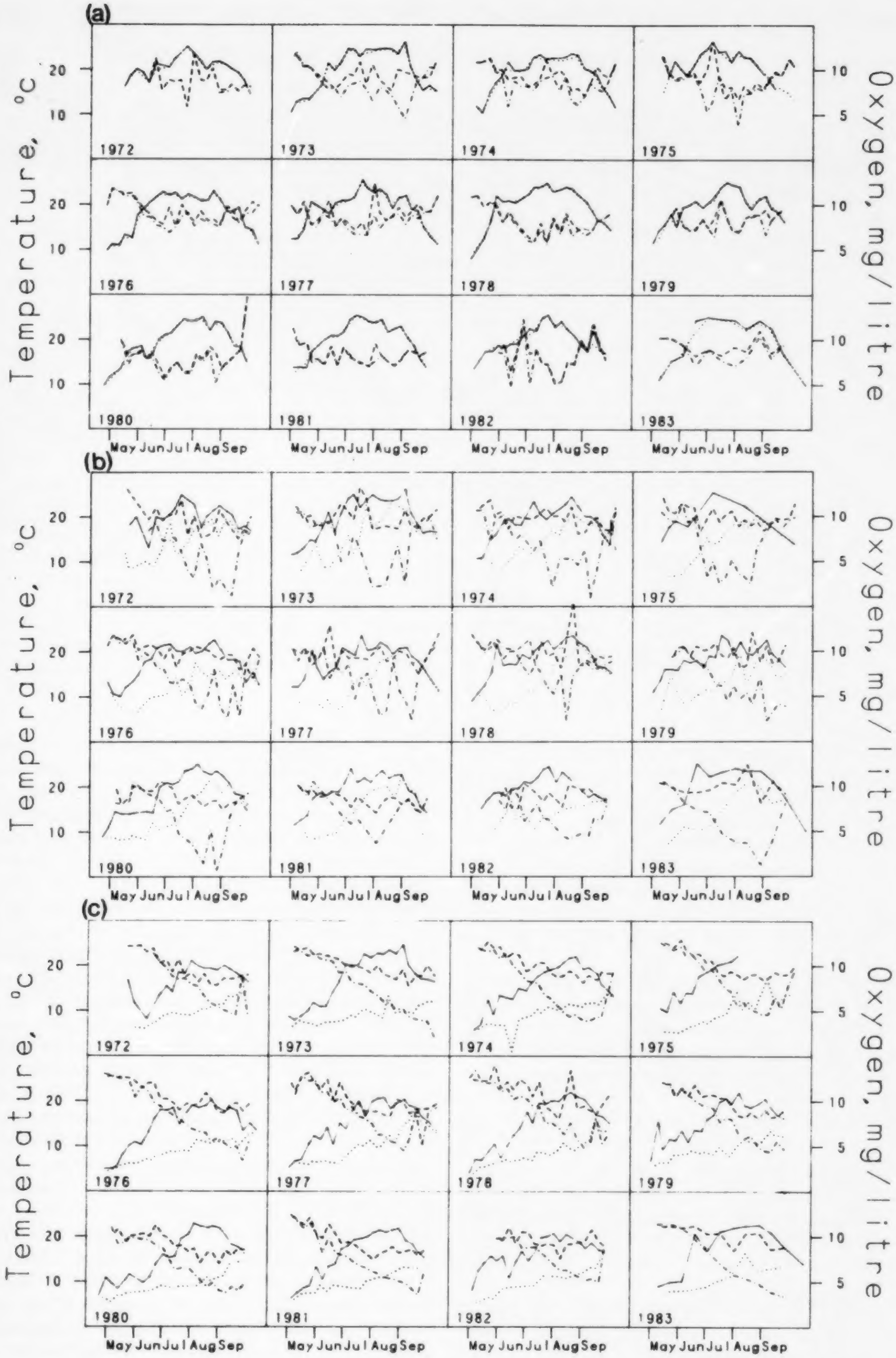

FIG. 2. Seasonal patterns of surface and bottom temperature and oxygen values at (a) Belleville, (b) Hay Bay, and (c) Conway, 1972–83 (—, surface temperature; - - -, surface oxygen; ···, bottom temperature; -·-, bottom oxygen).

TABLE 1. Percent frequency distribution by percent oxygen saturation and temperature ranges in four regions of the Bay of Quinte, 1967–83 (using all available data).

Area[a]	Temperature range	Percent oxygen saturation[b]			Total
		60	100		
1		0.1	12.9	10.9	23.9
	15–	0.7	16.7	11.7	29.1
	20–	1.0	25.9	15.7	42.6
	25–	0.1	1.9	2.4	4.4
	Total	1.9	57.4	40.7	N = 2422
2		0.8	10.9	6.5	18.2
	15–	3.2	22.4	10.5	36.1
	20–	2.2	19.7	19.2	41.1
	25–	0.2	1.2	3.2	4.6
	Total	6.4	54.2	39.4	N = 1491
3		2.9	26.9	6.6	36.4
	15–	6.5	19.2	13.8	39.4
	20–	1.9	10.4	11.1	23.5
	25–	—	—	0.7	0.8
	Total	11.3	56.5	32.2	N = 2593
4		11.5	34.7	11.2	57.4
	15–	2.8	19.6	10.4	32.8
	20–	0.4	3.7	5.6	9.7
	25–	—	—	0.1	0.1
	Total	14.7	58.0	27.3	N = 11130

[a] 1, Trenton to Telegraph Narrows; 2, Telegraph Narrows to Long Reach; 3, Picton and Hay bays; 4, Adolphus Reach.

[b] Calculated using the saturation equation of Forstner and Gnaiger (1983).

evident below the thermocline. In many years, there are instances of oxygen levels being lowest at intermediate depths, e.g. ≃20 m in August 1977 and 1980 (Fig. 3a, 3b). Such midwater oxygen minima are consistent with the elevation of nitrite levels found (Project Quinte unpublished data, 1978–83) at mid-depths (15–20 m) at Conway in August and September in a number of years. This suggests that nitrification was occurring.

Hypolimnetic Warming and Oxygen Depletion

We carried out two types of data analysis: (i) regression-type covariance analysis (ANCOVA) of trends in water below 15 m depth at the Conway station and throughout Adolphus Reach, with years as treatments and a selection of covariates including Julian day of the year less 150 (DOY), sample depth (Z_s), Temp (temperature at Z_s), and their cross-products, and (ii) regression analysis of bottom temperature and oxygen levels against DOY at Hay Bay, Glenora, and Conway.

For covariance analyses, data selection was restricted to sample depths greater than 15 m between the Julian dates 160 (June 7–8) and 250 (September 5–6) for the years 1967–83. We found by inspection that prior to day 160 there was little vertical stratification and after day 250 there were often signs of deep mixing and/or overturn.

The covariance analysis for all temperature data combined shows that the warming of the hypolimnion is predicted (R^2 = 0.42) by the covariates DOY, Z_s, and DOY·Z_s (Table 2). The treatment (year-to-year) differences are significant (F = 8.7) but less so than the covariates. The average warming rate (degrees Celsius per day), according to the covariance regression equations, is a simple function: $0.1415 - 0.0024 \cdot Z_s$ (Table 2). At 20 m, this predicts a warming rate of $0.094°\mathrm{C \cdot d^{-1}}$, while at 50 m the rate is $0.022°\mathrm{C \cdot d^{-1}}$.

The covariance analysis for all oxygen data combined shows that oxygen depletion in the hypolimnion is largely predicted (R^2 = 0.80) by DOY and Temp (Table 2). A cross-product term, DOY·Temp, is also significant (F = 21.2). The treatment (year-to-year) differences are significant although their contribution to explaining variance is much less than that of the covariates. Significant treatment differences only point to elevation differences in regression equations and not differences in slopes, e.g. rates of change with covariates. The significance of the positive DOY·Temp cross-product term in the oxygen ANCOVA suggests that oxygen depletion rates are lower at higher temperatures. The contribution of temperature alone is to set the initial conditions; the higher the termperature at the onset of stratification, the lower the initial oxygen. According to the oxygen covariance regression equations, at a fixed hypolimnion temperature of 10°C, the oxygen depletion rate, regardless of depth, will be $68.6\ \mathrm{mg \cdot m^{-3} \cdot d^{-1}}$. At a fixed temperature of 15°C, the rate will be $64.8\ \mathrm{mg \cdot m^{-3} \cdot d^{-1}}$. Given that the hypolimnion typically warms from 10 to 15°C over the period of stratification, no appreciable affect of temperature on oxygen depletion will be detectable (below it will be shown that confidence intervals on oxygen depletion rates are typically $\pm 5-10\ \mathrm{mg \cdot m^{-3} \cdot d^{-1}}$ and often higher).

The covariance analyses for temperature and oxygen data collected at the Conway station show results (Table 3) similar to those for the whole of Adolphus Reach. The warming trend is largely predicted (R^2 = 0.80) by DOY and DOY·Z_s with a small but significant contribution due to treatments (years). Oxygen depletion is explained (R^2 = 0.87) almost entirely by DOY with a lesser but significant contribution due to years (treatments). The covariance regressions predict a warming rate at 30 m, the typical depth of the Conway station, of $0.055°\mathrm{C \cdot d^{-1}}$ with an oxygen depletion rate of $65.2\ \mathrm{mg \cdot m^{-3} \cdot d^{-1}}$. Sample depth ($Z_s$) was unimportant with respect to oxygen depletion and barely so with respect to warming. So, analysis of bottom oxygen and temperature trends should reflect trends throughout the hypolimnion at each station.

Regression analysis of bottom temperature and oxygen trends was performed with data from the Hay Bay, Glenora, and Conway stations. For Conway, the earlier data of Tucker (1948) and McCombie (1967) were also analyzed. Once again, only data collected between Julian days 160 and 250 were included.

The bottom warming rates are highest at Hay Bay, in between at Glenora, and lowest at Conway (Table 4). This is consistent with the station depths and the depths to which mixing extends late in the summer. Oxygen depletion rates are most variable at Hay Bay, consistently high at Glenora, and intermediate for both variation and level at Conway (Table 4). There is no significant relationship between warming rates and oxygen depletion rates (r = 0.27, ns at P = 0.05). The historical trend in oxygen depletion rates (Fig. 4) at Conway does support the idea of increasing depletion with increasing phosphorus loading. However, this interpretation depends heavily on the 1945 point.

Oxygen Depletion and Eutrophication

To examine the influence of eutrophication on oxygen depletion, we compiled a data set for Conway and Adolphus Reach, reflecting both physical and eutrophic characteristics (Appen-

TABLE 2. Covariance analysis results for temperature and oxygen in Adolphus Reach (all sample depths 15 m, Julian days 160–250 inclusive, 1967–83).

	Temperature (°C)				Oxygen ($mg \cdot L^{-1}$)			
Source	Coeff.	df	MS	*F*	Coeff.	df	MS	*F*
Covariates[a]		3	12845.4	999.1		3	3342.3	3878.7
DOY	0.1415	1	6542.3	508.9	−0.0762	1	1339.6	1554.6
Z_s	−0.0660	1	361.8	28.1	n.u.	—	—	—
DOY·Z_s	−0.0024	1	1792.1	139.4	n.u.	—	—	—
Temp	n.u.	—	—	—	−0.0540	1	30.1	35.0
DOY·Temp	n.u.	—	—	—	0.0008	1	18.2	21.2
Years		16	111.1	8.7		16	91.8	106.5
Residual		4305	12.9			3342	0.9	
Total		4324	22.1			3361	4.3	
R^2				0.42				0.80

[a] DOY = Julian day of the year − 150; Z_s = sample depth (m); Temp = temperature at Z_s; n.u. = not used in analysis; R^2 = percentage of variance accounted for by covariates and treatments.

TABLE 3. Covariance analysis results for temperature and oxygen at Conway (all Z_s 15 m, Julian days 160–250, 1967–83).

	Temperature (°C)				Oxygen ($mg \cdot L^{-1}$)			
Source	Coeff.	df	MS	*F*	Coeff.	df	MS	*F*
Covariates		2	3599.1	1654.1		1	1229.0	2567.7
DOY	0.2173	1	6693.0	3075.9	−0.0652	1	1229.0	2567.7
Z_s	n.u.	—	—	—	n.u.	—	—	—
DOY·Z_s	−0.0054	1	3563.8	1637.8	n.u.	—	—	—
Temp	n.u.	—	—	—	n.u.	—	—	—
Years		13	24.8	11.4		13	16.0	31.6
Residual		868	2.2			436	0.5	
Total		883	10.7			450	3.8	
R^2				0.80				0.87

dix, Table A2). Conway was selected first because we had results there for the greatest number of years. The bottom oxygen depletion rates were taken to be estimates of VHODs, the volume-based hypolimnetic oxygen depletion rates, since the covariance analyses had shown that depth (Z_s) was not an important factor. AHODs, area-based rates, were calculated as the product of the VHOD and the hypolimnion thickness (Z_h). The thickness of the hypolimnion was assumed to be equal to the difference between the summer mean depth (Z_{mix}) at which the maximum vertical density occurs (E. S. Millard, Great Lakes Fisheries Research Branch, pers. comm.) and the summer mean station depth. These estimates of Z_h are likely too great, since they ignore any mesolimnion given that Z_{mix} is the epilimnion thickness. However, oxygen depletion was usually apparent in the mesolimnion and the distinction between meso- and hypolimnia was rarely clear.

We calculated correlations between VHODs and AHODs and the physical and eutrophication indicators. The best correlations with VHOD were due to mean summer light extinction (ϵ) (r = 0.65), mean summer river runoff (Q) (r = −0.56), and mean summer Secchi depth (r = −0.55) (Table 5). With AHOD, the best were due to mean euphotic zone (Z_{eu}) (r = −0.78), summer phosphorus loading uncorrected for Lake Ontario backflow (Z_{pn}) (r = 0.73), and mean summer total phosphorus (r = 0.65). The VHOD was also correlated with the summer mean hypolimnion temperature ($\bar{T}_h$) (r = 0.422).

Elsewhere, similar correlations have been obtained (Table 6). Charlton (1980) obtained a predictive equation involving Chl a, Z_h, and $\bar{T}_h$. Applied to our Conway data, we found that the predictions were not significantly correlated with actual values (r = 0.50, ns at P = 0.10, N = 11). Vollenweider and Janus (1982) presented two predictive equations. The first involves Chl a, Z_{eu}, and $\bar{Z}$. We obtained no correlation (r = −0.01, ns at P = 0.10, N = 11). The second involves gross primary production (PP), Z_{eu}, and $\bar{Z}$. We obtained a significant correlation (r = 0.56, significant P = 0.10, N = 11).

When we calculated correlations between VHOD and AHOD, and physical and eutrophication indicators for Hay Bay and Glenora (Table A3), the results were not the same (Table 5). There were few significant correlations and none with eutrophication indicators. This reinforces Vollenweider and Janus' (1982) argument that empirical predictive models based on studies of many lakes rarely work in time-series studies.

Discussion

These analyses show that oxygen depletion rates in the lower part of the Bay of Quinte did not decline in response to large decreases (≈70%) in point-source phosphorus after 1977 (Minns et al. 1986). The analyses also show that the hypolimnetic warming rates or mean hypolimnetic temperature did not consistently influence the oxygen depletion rates. At Conway, $\bar{T}_h$ was negatively correlated with VHOD, while at Glenora the correlation was positive.

The correlations between oxygen depletion and eutrophication indicators were contradictory. At Conway, they implied that with decreased nutrient loading, oxygen depletion would decrease. However, at Conway and the other two stations, there is no evidence of a decrease in oxygen depletion since 1977. Robinson (1986) found little evidence of changing water quality

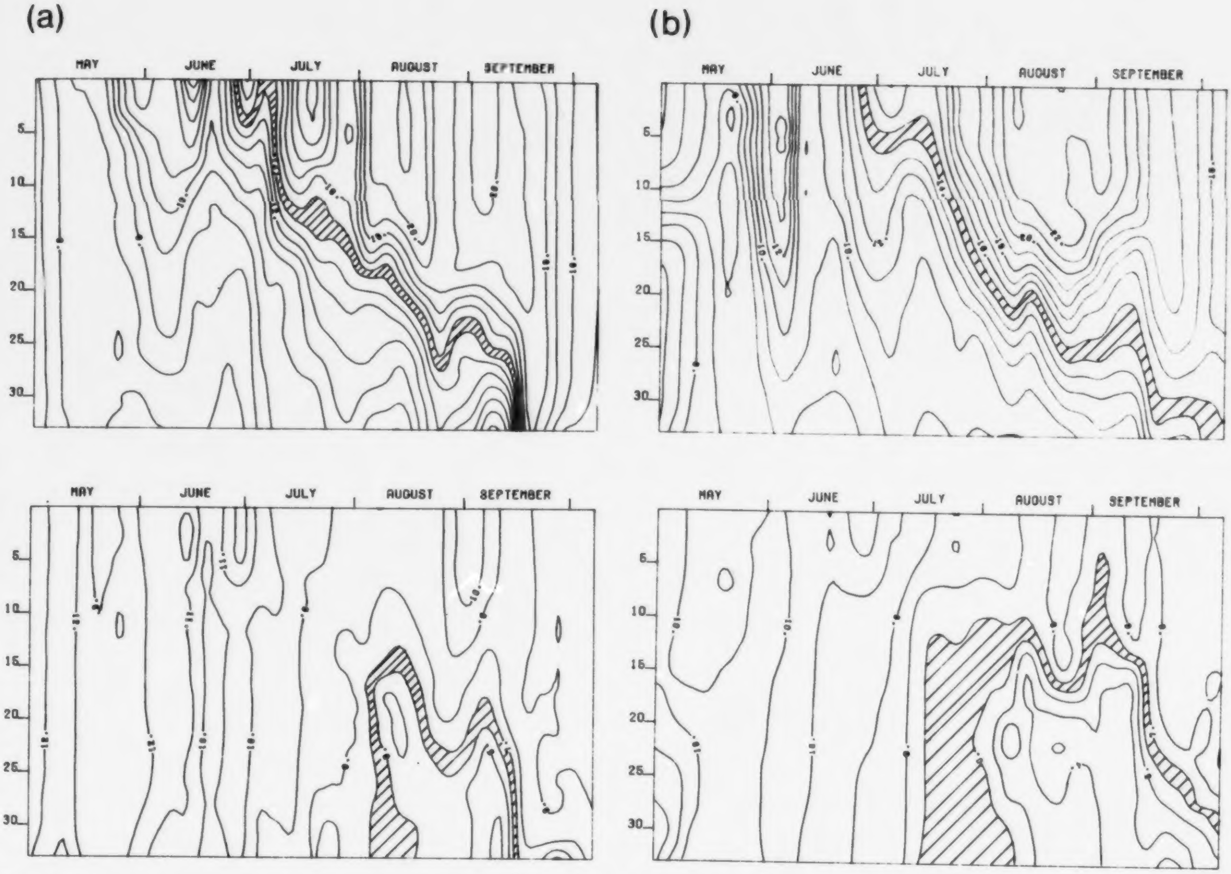

FIG. 3. Seasonal temperature (upper) and oxygen (lower) isopleths at Conway in (a) 1977 and (b) 1980 (cross-hatchng at 14–15°C and 6–7 mg $O_2 \cdot L^{-1}$).

in Adolphus Reach following implementation of phosphorus controls in 1978. Minns et al. (1986) showed, in an analysis of nutrient budgets in the Bay of Quinte, that the nutrient regime is controlled in the lower Bay by exchanges with Lake Ontario and by internal loading. Millard and Johnson (1986) were not able to demonstrate significant changes in primary production or light extinction (ϵ) in the lower Bay. They also showed that there is a high background light extinction, not due to algae, which elsewhere (Lasenby 1975) has been considered evidence of allochthonous matter, particulate and dissolved. Johnson and Brinkhurst (1971) presented evidence of the importance of allochthonous imports to the benthic community metabolism in the Bay of Quinte. So, there is little evidence of change in the trophic state of the lower Bay of Quinte, and the observed oxygen depletion rates are consistent.

Physical factors (e.g. $\overline{T}_h$, warming rate, and exchanges with Lake Ontario) do not appear to greatly influence oxygen depletion rates. In Lake Erie, Charlton (1980) showed that hypolimnion thickness and temperature did affect oxygen depletion. However, this was in the central basin where the average hypolimnion thickness is ≃3–4 m (Vollendweider and Janus 1982). In the lower Bay of Quinte, there is a large hypolimnion which tends to offset such effects.

At Conway, the areal hypolimnetic oxygen depletion rate has averaged 1.37 ± 0.19 g $O_2 \cdot m^{-2} \cdot d^{-1}$. Of this rate, part is attributable to the warming of the hypolimnion, part to metabolism in the water column, and part to benthic metabolism.

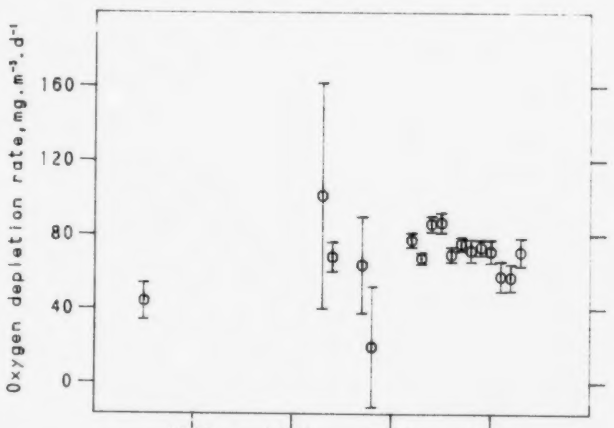

FIG. 4. Oxygen depletion rate (mean ± SE) by year at Conway.

Stratification generally sets in when the water column is at about 10°C and the warming generally raises the hypolimnion temperature to 15°C after about 100 d. If there was no metabolic depletion and the oxygen levels remained at saturation, the absolute level would decline from 11.29 to 10.09 mg $O_2 \cdot L^{-1}$, about 0.23 $g \cdot m^{-2} \cdot d^{-1}$. Thus, the metabolic part of AHOD

TABLE 4. Temperature and oxygen trends in bottom waters at three stations.

		Temperature					Oxygen				
Year	$\bar{Z}_b$[a]	N	$\hat{a}$	$\hat{b}$	S_b	r	N	$\hat{a}$	$\hat{b}$	S_b	r
Hay Bay											
1972	10.9	8	8.87	0.0845	0.0269	0.789	9	9.93	−0.0746	0.0202	−0.813
1973	11.6	10	7.50	0.1530	0.0178	0.950	9	9.39	−0.0821	0.0205	−0.834
1974	11.7	10	8.41	0.1300	0.0226	0.897	9	8.34	−0.0485	0.0218	−0.643
1975	11.8	13	9.12	0.1229	0.0169	0.910	13	7.06	−0.0331	0.0264	−0.354
1976	12.5	13	8.06	0.0883	0.0178	0.831	13	9.63	−0.0561	0.0141	−0.768
1977	11.6	11	4.77	0.1613	0.0265	0.897	11	8.92	−0.0547	0.0199	−0.675
1978	11.3	10	5.14	0.1652	0.0226	0.933	10	11.04	−0.0790	0.0214	−0.794
1979	10.9	12	7.93	0.0987	0.0245	0.787	12	10.37	−0.0785	0.0083	−0.949
1980	11.7	10	7.02	0.1413	0.0192	0.934	10	10.81	−0.1042	0.0127	−0.945
1981	11.2	8	8.07	0.1413	0.0277	0.902	4	9.25	−0.0781	0.0261	−0.904
1982	10.9	10	13.09	0.0159	0.0248	0.222	10	9.38	−0.0551	0.0131	−0.830
1983	12.4	6	6.04	0.1713	0.0282	0.950	6	9.51	−0.0842	0.0102	−0.972
Glenora											
1972	21.0	11	7.22	0.0782	0.0212	0.776	12	13.12	−0.1006	0.0081	−0.969
1973	23.4	12	6.56	0.1231	0.0271	0.820	13	11.50	−0.1042	0.0079	−0.970
1974	21.3	11	7.56	0.1009	0.0192	0.868	11	11.48	−0.0997	0.0115	−0.945
1975	23.5	13	4.53	0.1172	0.0150	0.920	13	11.13	−0.0972	0.0088	−0.957
1976	22.0	12	6.09	0.1042	0.0146	0.914	12	11.48	−0.0824	0.0089	−0.947
1977	19.2	12	4.03	0.1512	0.0217	0.911	12	11.09	−0.0656	0.0146	−0.819
1978	20.9	13	4.77	0.1321	0.0165	0.924	13	12.09	−0.0937	0.0099	−0.944
1979	20.7	13	6.61	0.0867	0.0173	0.834	13	11.74	−0.0940	0.0079	−0.964
1980	21.8	11	6.14	0.1032	0.0136	0.930	11	11.09	−0.1043	0.0098	−0.963
1981	22.0	11	6.47	0.1059	0.0157	0.914	6	10.37	−0.0943	0.0078	−0.987
1982	21.3	10	7.00	0.0702	0.0473	0.465	11	10.06	−0.0494	0.0115	−0.817
Conway											
1945[b]	—	11	7.51	0.0510	0.0210	0.822	7	10.44	−0.0440	0.0100	−0.979
1963[c]	—	9	7.41	0.0070	0.0080	0.645	7	15.04	−0.1010	0.0610	−0.884
1964[c]	—	15	7.84	0.0360	0.0090	0.931	15	11.23	−0.0680	0.0080	−0.980
1967	33.8	4	7.40	0.0143	0.0161	0.534	4	9.29	−0.0636	0.0260	−0.866
1968	34.0	9	10.01	0.0302	0.0162	0.575	7	9.57	−0.0194	0.0326	−0.257
1972	31.9	12	6.40	0.0510	0.0080	0.896	12	12.68	−0.0772	0.0039	−0.988
1973	34.5	12	7.03	0.0402	0.0177	0.584	12	11.43	−0.0674	0.0030	−0.990
1974	34.3	13	4.84	0.0785	0.0221	0.731	13	11.75	−0.0858	0.0042	−0.987
1975	29.8	13	4.81	0.0908	0.0161	0.862	12	12.41	−0.0866	0.0054	−0.981
1976	34.9	13	6.04	0.0571	0.0076	0.915	13	11.76	−0.0693	0.0040	−0.982
1977	30.6	13	4.92	0.0831	0.0134	0.882	13	12.09	−0.0751	0.0037	−0.987
1978	33.1	13	5.97	0.0459	0.0089	0.841	13	12.34	−0.0715	0.0061	−0.962
1979	31.8	13	7.68	0.0347	0.0109	0.694	13	11.86	−0.0733	0.0042	−0.983
1980	34.3	10	7.46	0.0306	0.0078	0.811	10	10.74	−0.0711	0.0062	−0.971
1981	32.7	9	6.83	0.0532	0.0115	0.867	6	10.14	−0.0576	0.0082	−0.962
1982	30.3	7	7.96	0.0432	0.0123	0.844	7	10.85	−0.0570	0.0072	−0.962
1983	29.7	6	6.49	0.0839	0.0355	0.763	6	10.92	−0.0707	0.0075	−0.978

[a] $\bar{Z}_b$ = mean bottom depth.

[b] Tucker (1948).

[c] McCombie (1967).

may be estimated at 1.14 g $O_2 \cdot m^{-2} \cdot d^{-1}$. Johnson and Brinkhurst (1971) reported a mean sediment oxygen consumption rate at Conway of 0.22 g $O_2 \cdot m^{-2} \cdot d^{-1}$ at 10.8°C, which is 19% of the metabolic AHOD. So, a good portion of the organic matter falling out of the epilimnion is metabolized before it reaches the bottom sediments, thereby contributing to the recycling of nutrients which are returned to the epilimnion by the Lake Ontario backflow and upwelling (Minns et al. 1986). Adolphus Reach production is primed by nutrient exports from the upper Bay but maintained by the recirculation of nutrients: the "nutrient pump" (Minns et al. 1986). This imparts a stability to the eutrophication indicators, e.g. primary production and oxygen depletion. The mixing of the hypolimnion as reflected by the warming ensures that an ample supply of oxygen is brought in whether by vertical exchange with the epilimnion or by horizontal exchange with the hypolimnion in the outlet basin of Lake Ontario.

The analyses of phosphorus dynamics in the Bay of Quinte (Minns et al. 1986; Minns 1986b) point to a lengthy recovery period following a reduction in point-source loading; the lag is due to the internal loading from sediment phosphorus pools which take a long time to come to a new steady state. In Adolphus Reach, oxygen depletion rates reflect this lag.

Elsewhere the response of oxygen depletion to changing nutrient and inputs has been equivocal. Dillon et al. (1978) found that there was a decrease in oxygen depletion in Gravenhurst Bay, Ontario, following a large decrease in nutrient loading. The decrease was correlated with the decrease in algal biomass. Welch (1977) reported that diversion of one third of the phosphorus loading from Lake Sammanish, Washington, did

TABLE 5. Correlations between oxygen depletion rates and physical and eutrophication indicators at three stations (*significant at $P = 0.10$; **significant at $P = 0.05$; — = not calculated).

	Conway				Hay Bay				Glenora			
	VHOD		AHOD		VHOD		AHOD		VHOD		AHOD	
Variable	*N*	*r*	*N*	*r*	*N*	*r*	*N*	*r*	*N*	*r*	*N*	*r*
Year	16	0.19	11	−0.36	10	0.17	10	0.52	11	−0.49	11	−0.32
Warming	16	0.05	11	0.09	9	0.16	9	0.19	11	0.09	11	−0.15
$\bar{T}_h$	16	−0.42**	11	0.04	10	0.06	10	0.14	11	0.52	11	0.29
Secchi	16	−0.55**	11	−0.52	10	0.16	10	0.01	11	−0.39	11	−0.39
Chl *a*	13	0.27	11	0.21	10	−0.24	10	−0.04	11	0.15	11	0.00
Total P	13	−0.19	11	0.65**	10	−0.30	10	−0.44	11	0.45	11	0.31
ΣPP	11	0.49	11	0.30	10	−0.22	10	−0.38	11	0.43	11	0.29
ϵ	11	0.65**	11	0.65**	—	—	—	—	—	—	—	—
Z_{eu}	11	−0.33	11	−0.78**	10	0.07	10	−0.21	11	−0.28	11	−0.22
Z_{mix}	11	0.43	11	−0.33	10	0.14	10	−0.39	11	0.62*	11	0.17
Q	15	−0.56**	11	0.55*	—	—	—	—	—	—	—	—
σ	11	−0.03	10	0.33	—	—	—	—	—	—	—	—
L_{pu}	11	0.14	10	0.73**	—	—	—	—	—	—	—	—
L_{pc}	11	−0.39	10	0.56*	—	—	—	—	—	—	—	—
—	—											
Station depth	13	−0.10	11	0.19	10	−0.19	10	0.06	11	0.44	11	0.69*

TABLE 6. Literature showing correlations of eutrophication measures with VHOD or AHOD.

Source	Variables
Cornett and Rigler 1980	AHOD – total P, ΣPP, Secchi depth
Cornett and Rigler 1979	AHOD – P retention, Z_h, hypolimnion temperature
Charlton 1980	AHOD – Chl *a*, Z_h, hypolimnion temperature
Vollenweider and Janus 1982	VHOD – Chl *a*, ΣPP, Z_{eu}, $\bar{Z}$
Welch et al. 1976	AHOD – σ, Chl *a*, total P, Secchi depth
Lasenby 1975	AHOD – Secchi depth
This study at Conway	VHOD – T_h, Secchi depth, ϵ, Q AHOD – total P, ϵ, Z_{eu}, Q, L_{pu}, L_{pc}

not bring any change in oxygen depletion. In Lake Washington, Edmondson (1966) found that oxygen depletion had not changed appreciably from 1930 to 1964 despite large increases in nutrient inputs and algal biomass. Finally, Charlton (1979) found little evidence of change in hypolimnetic oxygen depletion rates in the central basin of Lake Erie despite large trophic changes. The results of time-series studies of oxygen depletion in lakes under changing nutrient regimes differ from the empirical predictions obtained from multiple lake studies.

The discrepancy is likely due to lags in the response of lakes to changing nutrient inputs. Multilake studies look at the average condition of individual lakes, which likely reflects a steady state. In time-series studies, time must be allowed before a new steady state is established. The lag is due to sediment oxygen demand which is related to the enrichment of the sediments and internal nutrient loading. Our new hypothesis for the Bay of Quinte is that oxygen depletion rates will not decrease until internal nutrient loading decreases.

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References

CHARLTON, M. N. 1979. Hypolimnetic oxygen depletion in central Lake Erie: has there been any change? IWD Sci. Ser. 110, Ottawa, Ont.

1980. Hypolimnion oxygen consumption in lakes: discussion of productivity and morphometry effects. Can. J. Fish. Aquat. Sci. 37: 1531–1539.

CHRISTIE, A. E. 1973. Phytoplankton studies in the Bay of Quinte II. Physical, chemical and phytoplankton characteristics. Ont. Minist. Environ. Res. Rep. No. W44: 55 p.

CORNETT, R. J., AND F. H. RIGLER. 1979. Hypolimnetic oxygen deficits: their prediction and interpretation. Science (Wash., DC) 205: 580–581.

1980. The areal hypolimnetic oxygen deficit. An empirical test of the model. Limnol. Oceanogr. 25: 672–679.

DILLON, P. J., K. H. NICHOLLS, AND G. W. ROBINSON. 1978. Phosphorus removal at Gravenhurst Bay, Ontario: an 8-year study of water quality changes. Verh. Int. Ver. Limnol. 20: 263–271.

EDMONDSON, W. T. 1966. Changes in the oxygen deficit of Lake Washington. Verh. Int. Ver. Limnol. 16: 153–158.

FORSTNER, H., AND E. GNAIGER. 1983. Appendix A. Calculation of equilibrium oxygen concentration, p. 323. *In* H. Forstner and E. Gnaiger [ed.] Polarographic oxygen sensors. Springer-Verlag, Berlin.

FREEMAN, N. G., AND S. J. PRINSENBERG. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

HUTCHINSON, G. E. 1957. A treatise on limnology. Volume 1. Geography, physics and chemistry. Wiley, New York, NY.

JOHNSON, M. G., AND O. C. MCNEIL. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–84, p. 177–189. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

JOHNSON, M. G., AND R. O. BRINKHURST. 1971. Benthic community metabolism in Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1715–1725.

LASENBY, D. C. 1975. Development of oxygen deficit in 14 southern Ontario lakes. Limnol. Oceanogr. 20: 993–999.

MCCOMBIE, A. M. 1967. A recent study of the phytoplankton of the Bay of Quinte, 1963–1964. Proc. Tenth Conf. Great Lakes Res. 1967: 37–62.

MILLARD, E. S., AND M. G. JOHNSON. 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

MINNS, C. K. 1986a. Total phosphorus loading to the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. A simple whole-lake phosphorus model and its application to the Bay of Quinte, p. 84–90. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Tucker, A. 1948. The phytoplankton of the Bay of Quinte. Trans. Am. Microsc. Soc. 67: 365–383.

Vollenweider, R. A., and L. L. Janus. 1982. Statistical models for predicting hypolimnetic oxygen depletion rates. Mem. Ist. Ital. Idrobiol. 40: 1–24.

Welch, E. B. 1977. Nutrient diversion: resulting lake trophic state and phosphorus dynamics. U.S. EPA-600/3-77-003: 90 p.

Welch, H. E., P. J. Dillon, and A. Sreedharan. 1976. Factors affecting winter respiration in Ontario lakes. J. Fish. Res. Board Can. 33: 1809–1815.

Appendix: Physical and Eutrophication Indicators for Hay Bay, Glenora, and Conway Stations

For each station a number of physical and eutrophication indicators was compiled from this study and a number of other sources (Table A1). the data are presented for Conway (Table A2) and for Hay Bay and Glenora (Table A3).

Table A1. Physical and eutrophication indicators for the Bay of Quinte.

No.	Description	Name	Units	Source
1	Volume-based oxygen depletion (VHOD) rate	VHOD	$mg \cdot m^{-3} \cdot d^{-1}$	This study; Tucker 1948; McCombie 1967
2	Hypolimnion heating rate		$10^3 \cdot {}^\circ C \cdot d^{-1}$	McCombie 1967
3	Mean summer hypolimnion temperature	$\bar{T}h$	°C	McCombie 1967
4	Mean summer secchi depth		m	Tucker 1948; McCombie 1967; Robinson 1986
5	Mean summer chlorophyll *a*	Chl *a*	$mg \cdot m^{-3}$	Christie 1973; Robinson 1986
6	Mean summer total phosphorus		$mg \cdot m^{-3}$	Christie 1973; Robinson 1986
7	Annual gross primary production	ΣPP	$g\,C \cdot m^{-2} \cdot yr^{-1}$	Millard and Johnson 1986
8	Mean summer light extinction coefficient	ϵ	m^{-1}	Millard and Johnson 1986
9	Mean summer euphotic zone	Z_{eu}	m	E. S. Millard, unpubl. data
10	Mean summer mixed layer	Z_{mix}	m	E. S. Millard, unpubl. data
11	Mean summer river runoff	Q	$m^3 \cdot s^{-1}$	Minns 1986a
12	Summer flushing rate (May–September) including Lake Ontario backflow	σ		Minns et al. 1986
13	Summer phosphorus loading (uncorrected for backflow)	L_{pu}	$mg \cdot m^{-2} \cdot d^{-1}$	Minns et al. 1986
14	Summer phosphorus loading (corrected)	L_{pc}	$mg \cdot m^{-2} \cdot d^{-1}$	Minns et al. 1986
15	Area-based oxygen depletion rate (AHOD) calculated as VHOD × (station depth − mixer layer depth)	AHOD	$mg \cdot m^{-2} \cdot d^{-1}$	This study

Table A2. Compilation of data describing conditions at Conway station (see Table A1).

	Hypolimnion			Epilimnion							Lower BOQ			
Year	VHOD (1)	Warming (2)	Temperature (3)	Secchi (4)	Chl *a* (5)	Total P (6)	ΣPP (7)	ϵ (8)	Z_{eu} (9)	Z_{mix} (10)	Q (11)	σ (12)	L_{pu} (13)	L_{pc} (14)
1945	44	51	10.3	3.5	—	—	—	—	—	—	216.0	—	—	—
1963	101	7	7.9	2.6	—	—	—	—	—	—	102.6	—	—	—
1964	68	36	10.2	2.6	—	—	—	—	—	—	87.5	—	—	—
1965	64	14	8.0	2.5	5.1	38	—	—	—	—	186.6	4.02	3.6	6.3
1968	—	30	11.8	2.8	3.6	28	—	—	—	—	85.7	4.58	2.6	4.5
1972	77	51	9.5	3.0	9.0	23	351	0.64	8.0	12.3	219.5	4.20	3.9	4.6
1973	67	40	9.4	2.8	8.2	21	306	0.64	7.5	14.7	103.7	3.58	2.2	3.3
1974	86	79	9.1	2.5	5.9	24	289	0.72	6.5	13.7	170.5	6.16	3.2	4.3
1975	87	91	9.7	2.5	6.8	20	303	0.68	7.3	14.0	102.1	3.81	2.1	2.5
1976	69	57	9.0	2.9	7.8	20	298	0.61	8.0	15.8	114.4	5.63	2.1	3.8
1977	75	83	9.7	2.6	6.7	19	318	0.53	9.6	15.1	42.7	2.11	1.3	2.0
1978	72	46	8.6	3.2	4.8	18	213	0.63	8.7	18.2	112.6	6.36	1.6	2.1
1979	73	35	9.6	2.5	6.1	21	249	0.63	7.7	10.6	111.4	7.17	2.4	3.2
1980	71	31	9.3	2.7	6.3	23	243	0.66	7.3	14.8	130.6	6.87	1.5	3.2
1981	58	53	9.7	2.7	5.6	24	225	0.60	8.0	11.1	153.3	5.17	2.0	4.7
1982	57	43	9.9	2.9	5.4	19	248	0.55	8.1	7.1	138.2	—	—	—
1983	71	84	11.3	3.0	7.3	19	—	—	—	—	—	—	—	—

TABLE A3. Compilation of data describing conditions at Hay Bay and Glenora stations (see Table A1).

	Hypolimnion			Epilimnion					
Year	VHOD (1)	Warming (2)	Temperature (3)	Secchi (4)	Chl *a* (5)	Total P (6)	ΣPP (7)	Z_{eu} (9)	Z_{mix} (10)
Hay Bay									
1972	75	85	12.8	1.4	19.8	63	338	3.3	6.4
1973	82	153	15.0	1.6	23.4	53	386	3.8	6.2
1974	49	130	15.7	1.3	15.6	51	350	3.8	6.7
1975	—	123	15.7	1.1	23.6	56	433	3.4	6.7
1976	56	88	12.7	1.3	21.3	45	330	3.4	5.5
1977	55	161	13.0	1.6	28.1	47	344	4.0	5.2
1978	79	165	12.9	1.5	13.3	40	308	5.0	6.6
1979	79	99	13.2	1.4	18.3	34	235	3.9	5.8
1980	104	141	14.2	1.4	18.0	38	284	3.5	5.2
1981	78	141	16.1	1.3	16.4	46	259	3.7	5.0
1982	55	—	13.9	1.4	19.1	46	252	3.5	3.3
Glenora									
1972	101	78	11.9	2.0	12.6	38	400	5.0	9.5
1973	104	123	13.4	2.2	11.6	34	417	6.0	9.2
1974	100	101	12.8	1.8	10.8	34	395	4.9	10.3
1975	97	117	10.8	1.8	12.3	35	412	5.1	10.5
1976	82	104	11.2	2.0	12.5	30	394	5.5	8.0
1977	66	151	12.1	2.3	14.4	30	343	6.1	9.4
1978	94	132	12.2	2.2	9.6	27	303	7.0	9.6
1979	94	87	11.5	2.0	11.3	27	272	5.7	6.2
1980	104	103	12.2	2.0	9.6	25	314	6.2	10.0
1981	94	106	11.8	1.8	10.4	34	264	6.5	9.1
1982	49	70	10.8	2.1	7.7	25	254	6.3	5.7

Water Quality of the Bay of Quinte, Lake Ontario, Before and After Reductions in Phosphorus Loading

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Water quality improvements were immediately apparent in the Bay of Quinte following reductions in phosphorus loading from local sewage treatment plants. The upper portion of the bay is shallow and usually well-mixed by prevailing winds; most of the nutrient loading occurs here. After phosphorus controls became fully operational in 1977, reductions in total phosphorus of 28–38% and in total nitrogen of 13–20% were observed. Chlorophyll a levels also decreased, but there was no improvement in upper bay water clarity. The middle portion of the bay is slightly deeper and the lower portion much deeper than the upper bay; both sections are strongly influenced by wind-induced mixing, Lake Ontario incursions, and internal seiches. Water quality improvements were not as evident in these areas because of the dilutional effect of Lake Ontario. There was no change in total phosphorus levels, but soluble reactive phosphorus and chlorophyll a concentrations decreased. Inorganic nitrogen levels increased, thus increasing N:P ratios. There was no apparent change in water clarity in the middle or lower portions of the bay. Higher levels of total phosphorus and soluble reactive phosphorus in 1981 may reflect year-to-year variations or may indicate less than optimum removal of phosphorus at the wastewater treatment plants.

On a noté une nette amélioration de la qualité de l'eau de la baie de Quinte peu de temps après la réduction des rejets de phosphore des usines locales d'épuration des eaux usées. Les eaux de la partie supérieure de la baie sont peu profondes et généralement bien mélangées par les vents dominants ; c'est dans cette partie que s'effectuent la majorité des rejets de matières nutritives. Des baisses des teneurs en phosphore total de 28 à 38 % et de celles en azote total de 13 à 20 % ont été notées après la généralisation des mesures de lutte contre le phosphore, en 1977. Les teneurs en chlorophylle *a* ont aussi baissé, mais la transparence des eaux de la partie supérieure de la baie ne s'est pas améliorée. Par rapport à la partie supérieure, la partie médiane de la baie est légèrement plus profonde et la partie inférieure beaucoup plus. Le mélange des eaux de ces parties dépend fortement du mélange par le vent, des entrées d'eau en provenance du lac Ontario et du brassage par seiches internes. L'amélioration de la qualité de l'eau n'était pas aussi visible dans ces parties étant donné la dilution causée par les eaux du lac Ontario. Les teneurs en phosphore total sont demeurées inchangées mais celles en phosphore réactif soluble et en chlorophylle *a* ont diminué. Les teneurs en azote inorganique ont augmenté, augmentant ainsi le rapport N : P. La transparence des eaux des parties médiane et inférieure de la baie ne s'est pas améliorée de façon appréciable. Les teneurs en phosphore total et en phosphore réactif soluble plus élevées notées en 1981 peuvent s'expliquer par des variations annuelles ou une élimination du phosphore non optimale aux usines d'épuration des eaux usées.

Introduction

The Bay of Quinte is in an advanced state of eutrophication as a result of excessive nutrient loading from local municipalities. This condition has been developing since at least the 1940's (Tucker 1948). There is, however, a gradation in water quality between the upper bay (most productive) and lower bay (least productive) (Fig. 1). Over the years, water quality has deteriorated to a point that, at times, seriously impairs the use of the bay for recreation and as a source of water supply. Unsightly algal blooms have occurred frequently (Johnson and Owen 1971; McCombie 1967; Nicholls and Carney 1979), dissolved oxygen levels have been reduced in some areas (Tucker 1948; Minns and Johnson 1986), vast beds of rooted aquatic plants have disappeared (Crowder and Bristow 1986), and certain species of invertebrates and fish have been lost or replaced by less desirable species (Johnson and Brinkhurst 1971; Hurley and Christie 1977).

Phosphorus has been identified as the key nutrient governing the degree of eutrophy in a majority of the world's north-temperate lakes (Schindler 1977). In Ontario, prior to 1970, approximately 50% of the phosphorus contributed by municipal sewage was contained in detergents. Federal regulations reduced the phosphate content in laundry detergents to 5% (as P_2O_5) by January 1, 1973. Furthermore, the International Joint Commission's recommendation to reduce phosphorus loadings to the Great Lakes led to the development of a phosphorus removal program for wastewater treatment plants in Ontario by the Ministry of the Environment. According to the program, all communities discharging sewage into the bay were required to install facilities capable of reducing the total phosphorus concentration in their final effluent to 1 mg P/L or less. The implementation date proposed was December 31, 1975. Wastewater treatment plants at Belleville and the Canadian Forces Base (Trenton) were already reducing phosphorus in their final effluents at that time. The facilities at Picton became operational in 1976 and at Trenton and Deseronto in 1977. However, it was not until the winter of 1977–78 that strict operational guidelines were enforced at the wastewater treatment plants and the plants began to operate efficiently. The plant at Napanee underwent an expansion of facilities in 1983. Detailed loading information is given in Minns et al. 1986.

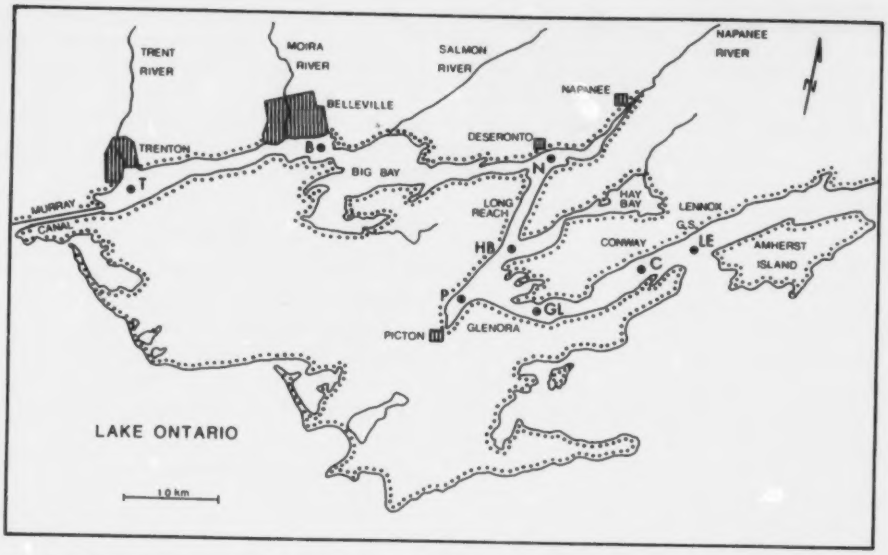

FIG. 1. Bay of Quinte showing the eight sampling stations: T, B, and N (upper bay), HB and P (middle bay), and GL, C, and LE (lower bay).

The current study of the bay, "Project Quinte," began in 1972. The period 1972–77 is regarded as the pre-phosphorus control period and 1978–81 as the post-phosphorus control period. The purpose of this paper is to examine the effects of phosphorus reductions at the wastewater treatment plants on the physical and chemical limnology of the bay. Changes in water quality that have occurred as a result of the reductions in phosphorus loading will be dealt with on a year-to-year, station-to-station, and seasonal basis.

Methods

Water samples were collected weekly from early May until late September or early October at five to eight stations along the bay (Fig. 1). Upper bay stations B and N, middle bay station N, and lower bay stations GL and C were regarded as the main stations and were sampled each year of the study. Station T (upper bay) was sampled minimally in 1979 and 1980, and eliminated in 1981. Station LE (lower bay) was added in 1975 to examine the possible effects of the Lennox hydro generating station on the bay. However, sampling here and at station P (middle bay) was discontinued after 1978 because of logistics and the similarity of other nearby stations.

Operations carried out at each station included the measurement of basic physical parameters, the collection of chemical and biological samples, and the estimation of primary production. The sequence of operations was almost identical at each sampling station and was repeated at approximately the same time of day from week to week and from year to year. Biological and primary production results are discussed elsewhere (Nicholls et al. 1986; Cooley et al. 1986; Millard 1986; Millard and Johnson 1986).

Temperature profiles were measured using a telethermometer (Applied Research Austin Inc., model FT3) which was calibrated against a standard centigrade thermometer (0.5°C accuracy). A YSI model 54 dissolved oxygen meter with a self-stirring probe (calibrated against air saturated distilled water) was used to determine oxygen concentrations in the euphotic zone and at 1 m above the bottom. At depths greater than 30 m, a Van Dorn sampler was used to bring water to the surface; temperature and dissolved oxygen were measured by inserting the probes into the Van Dorn sampler. In later years, a YSI model 54 meter with a submersible probe, or a Hydrolab model TDO-2 meter with a self-stirring submersible probe, was used to record both temperature and dissolved oxygen profiles. Water clarity was determined by use of a Secchi disc. Euphotic zone water samples were collected by lowering a narrow-mouthed 1-L bottle to twice the Secchi disc depth, the approximate location of 1% incident light intensity. The bottle was lowered and raised at a constant rate so that it filled completely just as it ascended to the surface. Samples for chemical analysis from 1 m above bottom were collected using a Van Dorn sampler; this sampling was discontinued at the upper bay stations (T, B, and N) in 1979 because near-even mixing in this area resulted in similar euphotic-zone and bottom-water chemistry. Beginning in 1978 samples were collected from mid-depth at the deeper stations (GL and C).

Samples for chemical analyses were refrigerated, and chlorophyll samples were filtered and frozen on the day of collection. All samples were shipped weekly to the Ministry of the Environment laboratory in Toronto where analyses were performed according to standard methods (American Public Health Association 1976).

Data analyses included analysis of variance, and the method of complete linkage developed by Sorensen (1948).

Results

Temperature and Dissolved Oxygen

In the upper bay, water temperature records from the Belleville water filtration plant indicated that above-freezing temperatures were usually reached by early to mid-April, but sometimes these occurred as early as mid-March. The shallow waters of the upper bay (4–8 m in midchannel) warmed quickly, usually reaching maximum temperature in July. Warmest temperatures were measured in 1975, and lowest seasonal maxima were in 1976. Stratification occurred during extended periods of calm sunny weather, but thermoclines were weak and unstable. The temperature difference between surface and bottom waters was usually 1°C or less. Dissolved oxygen levels in the upper bay were generally similar at all depths, except during periods of temporary stratification when concentrations were sometimes reduced to as low as 3.8 mg O_2/L at station B in early August. Supersaturated conditions occurred frequently at all three stations, and occasionally the entire water column was supersaturated with oxygen.

The middle bay is deeper (18 m maximum) and frequently developed distinct thermoclines, generally during the period mid-May to mid-July. However, surface water temperatures often lagged behind upper bay temperatures and maximum readings sometimes did not occur until August. By early August, thermoclines were depressed to just above the bottom or had disappeared completely. Lowest dissolved oxygen levels (minimum 0.6 mg O_2/L at station HB in August 1980) were recorded in or below the thermocline. Supersaturated oxygen conditions frequently developed in the euphotic zone and occasionally extended down to the thermocline or bottom.

The lower bay stratified during the summer months but even at the deepest point (60 m) the temperature gradient from surface to bottom was gradual. Here, maximum surface temperatures did not develop until August and were never as high as in the upper or middle bays. Again, supersaturated oxygen conditions frequently developed in the euphotic zone, or even throughout the epilimnion, and sometimes extended to the bottom during the earlier part of the year. A gradual lowering of oxygen levels near the bottom over the summer months indicated that there was little or no vertical mixing of near-bottom waters. Oxygen concentrations as low as 1.3 mg O_2/L were recorded at station GL in late August (1980). Dissolved oxygen conditions in the lower bay were examined more intensively by Minns and Johnson (1986).

Total Phosphorus

A gradation in total phosphorus (TP) existed between the upper and lower bays with the highest levels in the upper bay (Table 1). Relatively large year-to-year fluctuations were common during the pre-control years (Fig. 2). Pre-control concentatrations in the euphotic zone ranged from 52 to 89 μg P/L (seasonal means) in the upper bay, from 37 to 63 μg P/L in the middle bay, and from 18 to 38 μg P/L in the lower bay. These ranges of concentrations were similar to those reported by McCombie (1967) and Johnson and Owen (1971).

The reduction in phosphorus loading after 1977 resulted in substantial decreases in the TP levels at all upper and middle bay stations, and station GL (Fig. 2). TP concentrations were reduced by 28–38% in the upper bay, 20% in the middle bay, and 15% at station GL. Station C concentrations were unchanged. The initial drop in TP occurred immediately in 1978. However, in 1980 and 1981, TP concentrations began to increase again. At stations HB and GL the annual mean in 1981 approached the pre-control period average. At station C there was a gradual, but slight, decrease in mean TP from 1972 to 1978 (23–18 μg P/L) followed by a gradual increase to 24 μg P/L in 1981.

On a seasonal basis, maximum levels of TP measured during the May to September period were also affected by the reduced phosphorus loading. Upper and middle bay stations clearly showed a reduction in seasonal maxima (Fig. 3). In the lower bay, a wide range of concentrations was measured and overall there was a slight increase in seasonal maxima.

At station B, during the early years of the study, there were frequently high TP levels measured during late July and early August, followed by a decline in late August, and an increase to high levels again in September. After phosphorus controls were implemented, the midsummer extremes diminished, and in later years TP levels increased gradually from relatively low levels (24–30 μg P/L) in early May to a peak in September. Station HB responded in much the same way, although the midsummer peak was apparent only during the early years of the study. Higher near-bottom TP concentrations occurred more frequently during the latter half of the season. In the lower bay at station C, TP levels were generally low and uniform at all depths throughout the study. High concentrations were detected occasionally, but they were usually short-lived. Bottom water TP concentrations in late summer exceeded euphotic zone levels less often after phosphorus controls were in operation.

Soluble Reactive Phosphorus

Mean soluble reactive phosphorus (SRP) concentrations in the euphotic zone were high in the upper bay and decreased gradually toward the lower bay as in the case of TP. However, there was also a decline with time after 1972 at all stations which was probably related to detergent phosphorus legislation. Lowest mean values were recorded in 1979, ranging from only 1 to 2 μg P/L throughout the entire bay. Concentrations of SRP began to increase at all stations in 1980. By 1981, upper bay stations had average SRP levels as high as in 1972, and middle and lower bay stations were considerably higher than in 1972. Near-bottom concentrations followed a similar pattern but were not reduced as low in 1979. Lower bay stations had slightly higher average SRP concentrations near the bottom than in the euphotic zone, while upper and middle bay stations were similar at both depths. Many of the highest near-bottom concentrations were recorded at station LE. Mean mid-depth concentrations were always between the euphotic zone and near-bottom values.

During the early years of the study, SRP levels were low in the spring and climbed gradually over the summer to a peak in the fall (Fig. 4). Although the concentrations sometimes varied, the pattern was basically the same in the euphotic zone and near the bottom. As overall concentrations decreased, so did the fall peak, until near-uniform seasonal values were measured in 1979. In 1980, the higher fall levels began to reappear, and in 1981 much higher concentrations were measured at all stations and at all depths. These increases were probably related to the gradual increase in phosphorus loading from the six sewage treatment plants along the bay (Minns et al. 1986).

Nitrogen

In the four years since phosphorus controls were implemented there has been a reduction in total nitrogen (TN) of 13–20% in the upper bay and 3–4% in the middle bay, but an increase of 3–16% in the lower bay.

Seasonally there has been little change in pattern in the upper and middle bays; TN generally increased over the summer to reach maximum concentrations in August or September. The increase was not uniform, however, and there was frequently a depression in TN in late August. In the lower bay, TN concentrations have increased overall since phosphorus controls were implemented, with the largest increase occurring in May.

The overall decrease in TN was associated with a relatively large reduction in total organic nitrogen (TON) reflecting lower algal biomass (Nicholls et al. 1986; Nicholls and Carney 1986;

TABLE 1. Comparison of pre- and post-phosphorus control studies throughout the world. Note: sampling periods and depths may vary between lakes but are consistent for each individual lake.

	Total phosphorus (μg/L)		N:P ratio		Chlorophyll *a* (μg/L)		Secchi disc (m)		Survey period		Source
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	
Lake Ontario											
Bay of Quinte											
Stn. B	78	48	11.0	14.1	27.9	15.0	1.2	1.3	1972–77	1978–81	
Stn. N	70	46	12.7	16.7	29.3	19.8	1.2	1.2	1972–77	1978–81	
Stn. HB	53	40	14.3	17.5	22.0	16.5	1.4	1.4	1972–77	1978–81	
Stn. GL	33	28	16.7	20.5	12.4	10.2	2.0	2.0	1972–77	1978–81	
Stn. C	22	22	20.8	24.4	7.3	5.8	2.9	2.8	1972–77	1978–81	
Toronto Harbour	88	33							1968	1976–78	International Joint Commission 1978
Open water	23	16							1971–74	1979	Weiler 1981
Lake Erie											Dobson et al. 1974; Janus and Vollenweider 1981
Western basin	117	50							1968–73	1974–77	
Central basin	19	21							1970–73	1974–78	
Eastern basin	31	24	12.7	23.6	4.9	4.4			1973	1974–75	
Lake Muskoka											Dillon et al. 1978; G. W. Robinson, unpubl. data
Gravenhurst Bay	44	23	13.2	28.4	9.8	6.3	2.5	3.5	1969–71	1972–82	
Skaha Lake (B.C.)	30	22	8.6	16.0			4.5	4.2	1968–71	1973–81	Nordin 1983
Shagawa Lake (USA)	58	36			22	16	1.8	2.4	1971–72	1974–80	Larsen et al. 1979; Larsen and Malueg 1980
L. Washington (USA)	63	18			33	5	1.1	4.5	1961–63	1969–80	Edmondson and Lehman 1981
Lake Boren (Sweden)	41	18	13	34	10	6	1.5	1.9	1974	1975–76	Forsberg 1977; Forsberg et al. 1978
Lake Ekoln (Sweden)	78	46	15	41	25	10	1.6	2.0	1972	1973–76	Forsberg 1977; Forsberg et al. 1978
Lake Malaren (Sweden)	35	20					3.0	4.3	1965–69	1974–78	Forsberg and Ryding 1980
Lake Norrviken (Sweden)	270	180	15.6	12.9	151	90	0.6	0.8	1969	1970–76	G. Ahlgren 1978; I. Ahlgren 1978
Lake Vattern (Sweden)	10–15	7–8					7–8	10–12	1968–70	1978–80	Forsberg and Ryding 1980
Wahnbach Res. (Germany)							2.8	6.5	1969–70	1978–79	Bernhardt 1980

Millard and Johnson 1986). Total inorganic nitrogen (TIN) levels increased accordingly. In both the upper and lower bays, prior to phosphorus controls, there were extended periods when the TIN supply was almost exhausted. After 1978, particularly at station C, TIN levels were not reduced as severely. This represents an under-utilization of the available nitrate because of the lower algal densities. Ammonia levels were virtually unaffected (Fig. 5).

Reactive Silica

Before phosphorus controls were implemented, silica levels (as Si) were usually lowest in the spring and fall and highest during the late June to early August period. In 1978, however, tremendous increases were observed in the upper and middle bays. Springtime values were slightly elevated, but late summer concentrations rose as high as 10.7 mg/L at the Belleville station in early September. Silica levels were still high in early October at the end of the sampling period. There was a gradual decline after 1978 but concentrations in the upper bay remained high relative to the precontrol period average (Table 2). In the middle bay, summertime silica levels fluctuated considerably but the spring and early fall were marked by very low concentrations during the early years of the study. Again, in 1978, higher springtime values and very high fall levels were measured. A similar decline occurred after 1978, but concentrations were still high relative to the precontrol information. At station C, silica levels were initially very low all year, but by 1976, summer and fall concentrations were slightly higher. In 1978, much higher values were recorded in the spring and fall. By 1980, silica levels were again fairly uniform, but higher, throughout the season.

Chlorophyll *a* and Secchi Disc

A chlorophyll *a* concentration gradient similar to that of TP existed throughout the length of the Bay of Quinte. Prior to 1978, chlorophyll *a* concentrations in the euphotic zone ranged from 13.1 to 36.7 μg/L (seasonal means) in the upper bay, from 12.9 to 23.6 μg/L in the middle bay, and from 5.9 to 12.6 μg/L in the lower bay. The introduction of phosphorus controls resulted in an immediate drop in chlorophyll *a* concentrations at

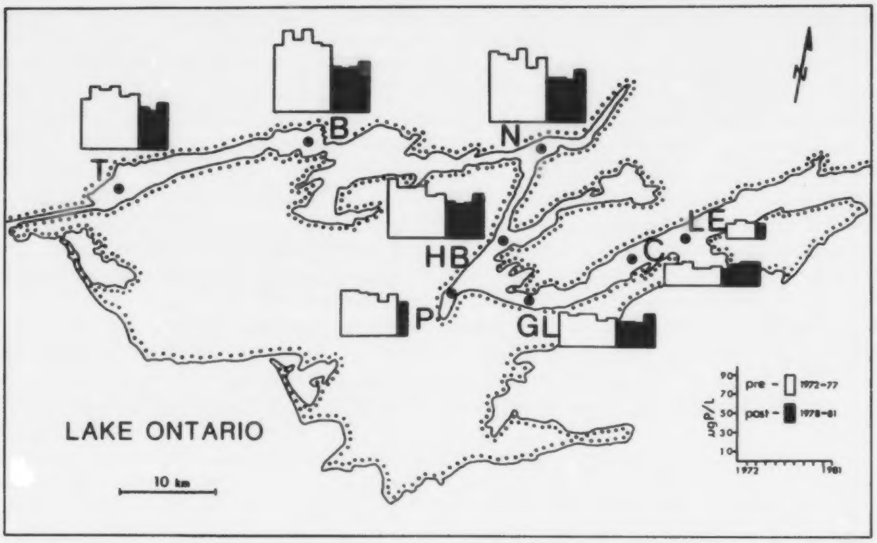

FIG. 2. Mean total phosphorus concentrations in the euphotic zone at all eight stations for the period 1972–81.

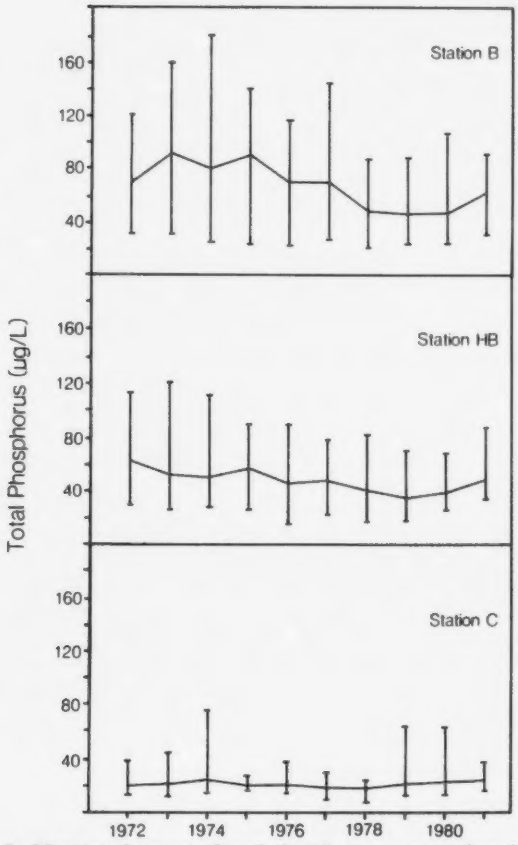

FIG. 3. Means and ranges of total phosphorus concentrations in the euphotic zone at stations in the upper (B), middle (HB), and lower (C) bays for the period 1972–81.

all stations. The greatest decrease was in the upper bay where 18–43% reductions occurred. In the middle bay, concentrations were reduced by 20%, and in the lower bay by 15–22% (Fig. 6a and 6b). Chlorophyll *a* is discussed more thoroughly in relation to primary production by Millard and Johnson (1986). Secchi disc readings were correspondingly lowest in the upper bay, and highest in the Conway to Lennox area. Over the 10 yr of the study there has been little or no change in mean Secchi disc readings at any station. Year-to-year variation was 0.9 m or less, with the greatest changes occurring at the lower bay stations.

Discussion

On the basis of morphology the Bay of Quinte has traditionally been divided into three sections: upper, middle, and lower bays. Sorensen's (1948) linkage method was used to demonstrate that the water at stations within each section is indeed chemically similar. The dendograms in Fig. 7 compare the annual means of TP, TN, and chlorophyll *a* for all years (1972–81) at all eight stations (T, B, N, HB, P, GL, C, and LE). More parameters could have been examined in this manner, but it was felt that these three were of fundamental importance and would be sufficient to demonstrate the relationships.

Clearly, upper bay stations B and N are much more similar to each other ($P < 0.05$) than either of them is to any other station or group of stations. Similarly, lower bay stations C and LE are closely linked to each other, and show the greatest degree of dissimilarity to the other stations. This is undoubtedly because of the greater depths and the influence of Lake Ontario on this portion of the bay (Minns et al. 1986). Station GL is considered a lower bay station but is actually more closely linked with the upper and middle bay groups. The middle bay is the least well defined. In the cases of TN and chlorophyll *a*, station T is closely linked with station HB, while on the basis of TP it is linked with stations B and N. However, this may be more of a coincidence than an actual linkage, since the presence of macrophytes and the dilutional effect of the Trent River greatly influence water quality conditions in this area. Station P is more closely linked with station HB than with station GL.

This analysis suggests that grouping the stations geographically is valid. The discrepancy with station T is explainable, and station GL seems to represent a transition between the

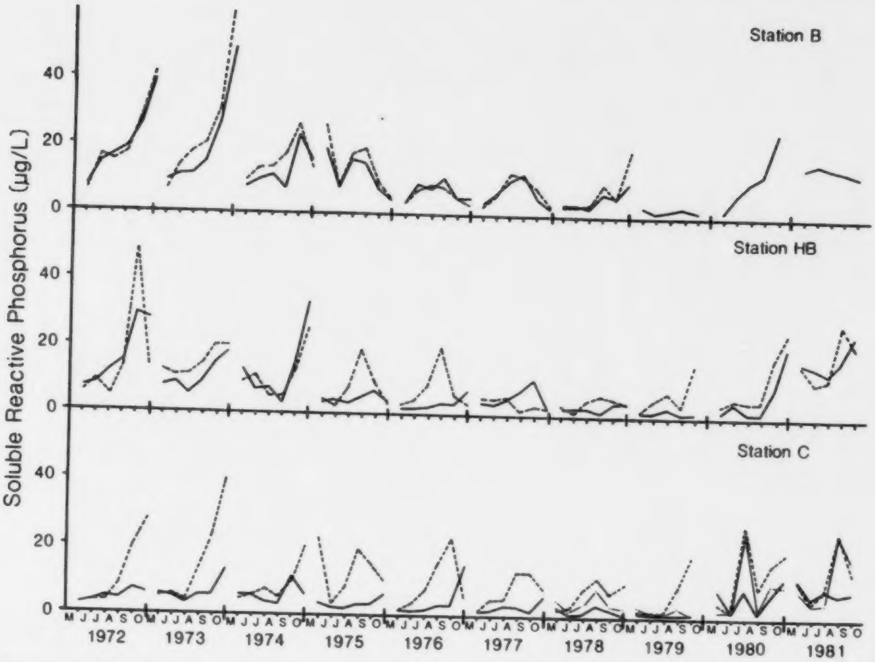

FIG. 4. Seasonal soluble reactive phosphorus concentrations at stations in the upper (B), middle (HB), and lower (C) bays for the period 1972–81. —, euphotic zone; ---, mid-depth; ---,1 m above bottom.

middle and lower bays. McCombie (1967) came to a similar conclusion on the basis of morphometry, physical–chemical conditions, and biological productivity.

Upper Bay

The upper bay was typically warm and well oxygenated throughout most of the summer season. This was due mainly to the shallowness of the area and strong prevailing winds which kept the bay well mixed from surface to bottom much of the time. Consequently, water quality characteristics were generally uniform throughout the water column. High primary production rates (Millard and Johnson 1986) and dense macrophyte beds in some areas (Crowder and Bristow 1986) helped to maintain high dissolved oxygen concentrations during the time of day when sampling took place.

All of the major rivers flowing into the Bay of Quinte enter via the upper bay and most of the municipalities discharging treated wastes are also located on this section of the bay. Therefore, it follows that the upper bay is most affected by external loading and any response to reduced phosphorus loading should be apparent first in the water chemistry of the upper bay. The implementation of phosphorus controls and improved sewage treatment facilities reduced TP loading from over 300 kg P/d to an average of 71 kg P/d for the period 1978–81 (Minns et al. 1986; Minns 1986).

As expected, the greatest reductions (28–38%) in TP occurred in the upper bay (Fig. 2). At the same time, a substantial reduction (13–20%) in TN occurred as a result of partial nitrogen removal which takes place during the process of phosphorus removal. An analysis of variance between seasonal means in the upper bay showed a clear-cut division between the pre- and post-control periods for TP, and to a lesser degree for TN.

The anticipated shift toward higher TIN levels because of lower algal biomass (Nicholls et al. 1986; Millard and Johnson 1986) was not immediately apparent in the upper bay, but after 1978 there were no longer sustained periods of very low TIN levels. The 15–41% increase in TN in 1981 was mainly due to a large increase in nitrate (Fig. 5). These higher nitrate levels may indicate inefficient plant operation as evidenced by higher loading (Minns et al. 1986) and higher ambient TP and SRP levels in the bay beginning in late 1980. Since less phosphorus is being removed in the treatment process, it should follow that less nitrogen (in the form of NH_3) is being removed. Nitrification of the wastewater after discharge to the bay would then result in higher nitrate levels.

Since the decrease in TP was greater than the decrease in TN, TN:TP ratios (by weight) increased slightly at all three upper bay stations, indicating an improvement in water quality. The change does not compare, however, with the improvement seen in eastern Lake Erie, Gravenhurst Bay, Skaha Lake, or Lakes Boren and Ekoln in Sweden (Table 1).

The decrease in TP was partly due to a decline in SRP. The fact that SRP declined gradually from 1972 until 1979 was probably a result of the phasing out of high-phosphate detergents, and the progressive improvement in efficiency of new plants as they were modified.

Lower chlorophyll *a* levels resulted from the decreased level of available phosphorus. The overall decrease in chlorophyll *a* was not sufficient to cause an improvement in water clarity as it did in other similar studies (Table 1).

A large proportion of the phytoplankton community in the upper bay consisted of diatoms (Nicholls and Carney 1979). With the decrease in chlorophyll *a* in 1978 came a corresponding increase in silica, since it was no longer being incorporated into diatom cells. The subsequent gradual decrease in silica represented a recovery of the diatom population (Nicholls et al. 1986).

As in Gravenhurst Bay the improvements in water quality occurred rapidly, just as in the Bay of Quinte, and a new steady

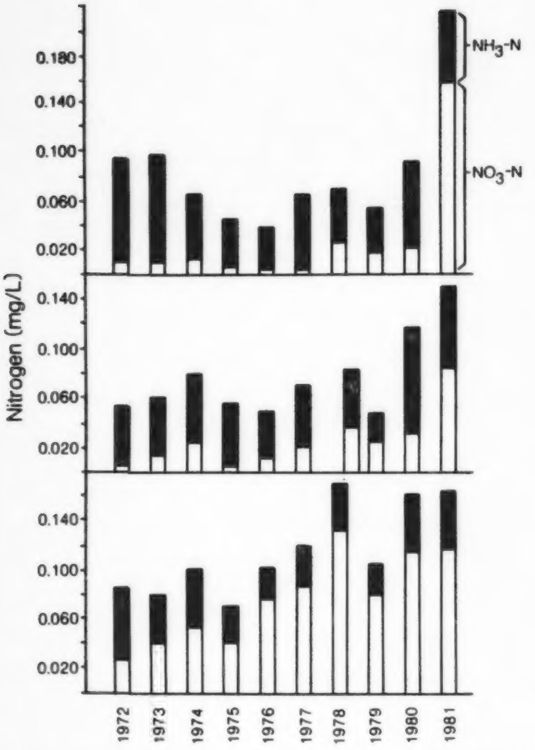

FIG. 5. Mean ammonia (NH_3) and nitrate (NO_3) concentrations in the euphotic zone at stations in the upper (B), middle (HB), and lower (C) bays for the period 1972–81.

TABLE 2. Mean silica concentrations (mg/L) from weekly euphotic zone sampling in the May to October period for the pre- (1972–77) and post- (1978–81) phosphorus control periods.

	B	N	HB	GL	C
1972–77	0.68	0.66	0.57	0.44	0.41
1978–81	2.51	1.89	1.46	0.90	0.74

state was soon established (Dillon et al. 1978; G.W. Robinson, unpubl. data). It was not until a new treatment plant, which operated inefficiently at first, was constructed at Gravenhurst that TP, chlorophyll *a*, and phytoplankton biomass began to increase again. In the Bay of Quinte, the rising TP in 1981, SRP in 1980–81, and the steady-decrease in silica after 1978 may be an indication that optimum phosphorus control is not being achieved at the plants. The Gravenhurst Bay case has shown that strict operational controls must be maintained at wastewater treatment plants. Fortunately, Gravenhurst Bay quickly reverted to its improved condition after the technical difficulties were resolved.

Middle and Lower Bays

The middle and lower bays were also strongly influenced by wind-induced mixing and additionally by cold-water incursions from Lake Ontario. Together they frequently created internal seiches that disrupted temperature and oxygen regimes and modified water chemistry (McCombie 1967; Freeman and Prinsenberg 1986; Minns and Johnson 1986). As a result, stratification in the middle bay lasted only until midsummer and most of the water column was well mixed for the remainder of the season. In the lower bay, unstable thermoclines allowed considerable vertical mixing and the hypolimnion became relatively warm. Minns et al. (1986) have hypothesized that these warmer temperatures may accelerate the breakdown of organic material produced in the euphotic zone or transported from upstream. With the next upsurge of hypolimnetic water these regenerated nutrients then become available for the current season's production. The fact that SRP levels tended to rise in the deeper waters of the lower bay lends support to this theory.

In most cases the Lake Ontario incursions tended to dilute the ambient chemical levels of the bay (e.g. iron). However, in the case of chloride, Lake Ontario levels were higher than those in the upper bay. The fact that elevated chloride levels were detected as far upstream as station HB demonstrated the magnitude of the Lake Ontario influence. The higher conductivity levels in the lower and middle bays were a result of the same influence. The diluting action of Lake Ontario was also responsible for the lower nutrient levels, initially, in the middle and lower bays compared with the upper bay. After 1978, tremendous improvements were apparent in the upper bay, but the improvement was not proportional farther downstream because of the moderating effect of Lake Ontario. TP concentrations in the open lake were typically 15 μg P/L during the summer months (Weiler 1981). This value is slightly lower than those measured in the Conway area, but compares well with the information available for Lennox. Nevertheless, the amount of available phosphorus (as SRP) in the lower bay decreased because less organic material was being transferred from the upper bay and subsequently decomposed in the hypolimnion of the lower bay. As a result, a decrease in phytoplankton populations occurred in the lower bay after 1978 even though TP remained about the same. Chlorophyll *a* levels were therefore lower, and the unused TIN increased (Fig. 5). TN therefore increased, and as a result, so did N:P ratios.

In the middle bay, the improvements in water quality in 1978 were probably due to a combination of the reduction in TP loading from upstream and the dilutional effect from downstream. The minimal change in TN in this area was indicative of the transitional nature of this part of the bay.

Conclusions

The Bay of Quinte has responded in a positive way to the reduced phosphorus loadings, but time will be required for chemical conditions to reach a new steady state. Certain physical and morphological features of the bay will tend to complicate the recovery mechanism by enhancing or restricting the various chemical and biological processes at work in the different sections of the bay.

The 1981 results may simply represent annual variation, but they may also be a forewarning of a reversion to pre-1978 conditions. Flushing rates were high from 1978 to 1980 (Minns et al. 1986) and this may have partially accounted for some of the improvements observed. However, Owen (1981) reported that phosphorus removal in the summer months of 1981 was less successful than in the previous two years.

It remains to be seen how long it will take the bay to stabilize chemically, and what role flushing has had on water quality improvements. But bearing in mind the Gravenhurst Bay study, it is absolutely essential that wastewater treatment plants be operated at optimum efficiency if long-term benefits are to be realized.

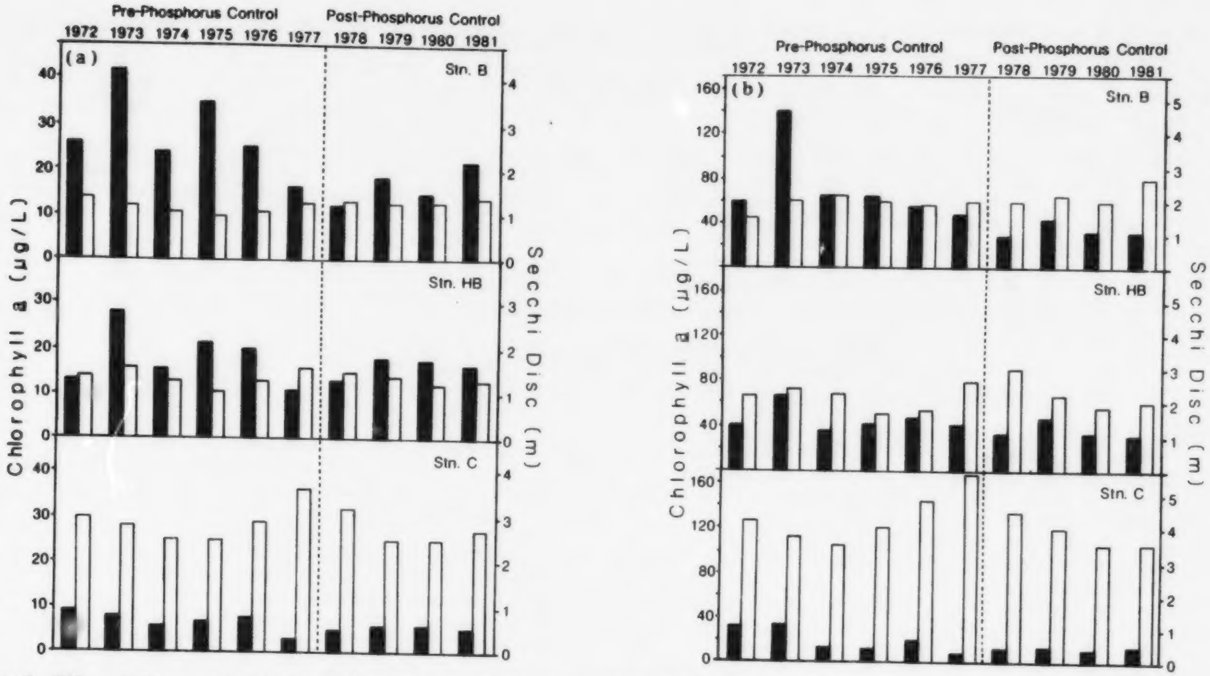

FIG. 6. Chlorophyll *a* concentrations (solid bars) in the euphotic zone and Secchi disc depths (open bars) at stations in the upper (B), middle (HB), and lower (C) bays for the pre- and post-phosphorus control periods. (a) Seasonal means; (b) Seasonal maxima.

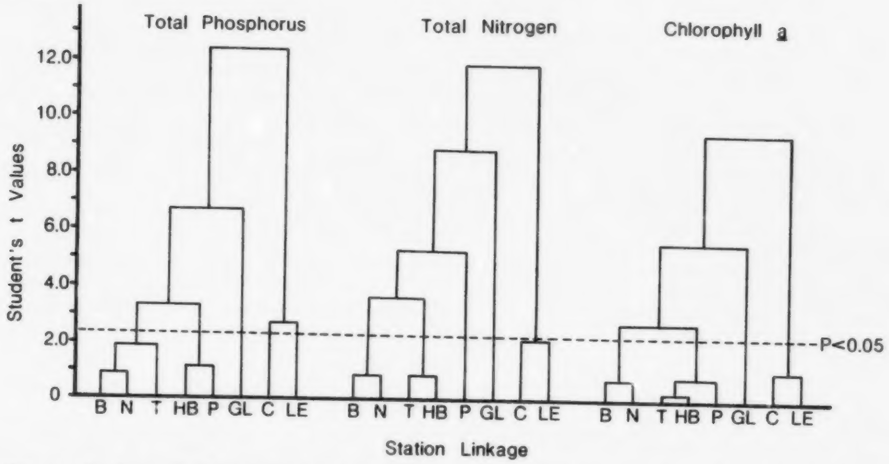

FIG. 7. Dendograms of student's *t* values from a station-to-station comparison of mean annual total phosphorus, total nitrogen, and chlorophyll *a* concentrations at the eight Bay of Quinte stations during the period 1972–81. Criteria for clustering followed Sorensen's (1948) method for complete linkage.

References

AHLGREN, G. 1978. Response of phytoplankton and primary production to reduced nutrient loading in Lake Norrviken. Verh. Int. Ver. Limnol. 20: 840–845.

AHLGREN, I. 1978. Response of Lake Norrviken to reduced nutrient loading. Verh. Int. Ver. Limnol. 20: 846–850.

AMERICAN PUBLIC HEALTH ASSOCIATION. 1976. Standard methods for the examination of water and wastewater. American Public Health Association, 1015 Eighteenth Street. N.W., Washington, DC. 20036.

BERNHARDT, H. 1980. Reservoir protection by in-river nutrient reduction, p. 272–277. *In* Restoration of lakes and inland waters. EPA 440/5-81-010. U.S. Environmental Protection Agency, Washington, DC.

COOLEY, J. M., J. E. MOORE, AND W. T. GEILING. 1986. Population dynamics, biomass, and production of the macrozooplankton in the Bay of Quinte during changes in phosphorus loadings, p. 166–176. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

CROWDER, A., AND M. BRISTOW. 1986. Aquatic macrophytes in the Bay of Quinte, 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

DILLON, P. J., K. H. NICHOLLS, AND G. W. ROBINSON. 1978. Phosphorus removal at Gravenhurst Bay, Ontario: an 8 year study on water quality changes. Verh. Int. Ver. Limnol. 20: 263–271.

Dobson, H. F. H., M. Gilbertson, and P. G. Sly. 1974. A summary and comparison of nutrients and related water quality in lakes Erie, Ontario, Huron and Superior. J. Fish. Res. Board Can. 31: 731–738.

Edmondson, W. T., and J. T. Lehman. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnol. Oceanogr. 26: 1–29.

Forsberg, C. 1977. Responses to advanced wastewater treatment and sewage diversion. Paper presented at Jubilee Symposium on Lake Metabolism and Lake Management, Uppsala, Aug. 22–27, 1977. National Swedish Environment Protection Board, Institute of Physiological Botany, Box 540, S-751 21, Uppsala, Sweden.

Forsberg, C., and S.-O. Ryding. 1980. Swedish experience of nutrient removal from wastewater, p. 298–303. *In* Restoration of lakes and inland waters. EPA 440/5-81-010. U.S. Environmental Protection Agency, Washington, DC.

Forsberg, C., S.-O. Ryding, A. Forsberg, and A. Claesson. 1978. Research on recovery of polluted lakes: improved water quality in Lake Boren and Lake Ekoln after nutrient reduction. Verh. Int. Ver. Limnol. 20: 825–832.

Freeman, N. G., and S. J. Prinsenberg. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Hurley, D. A., and W. J. Christie. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

International Joint Commission. 1978. Great Lakes Water Quality, Seventh Annual Report, Appendix B. Annual Report of the Surveillance Subcommittee, International Joint Commission, Windsor, Ont. 117 p.

Janus, L. L., and R. A. Vollenweider. 1981. The OECD Co-operative Programme on Eutrophication, Canadian Contribution. Sci. Ser. No. 131, National Water Research Institute, Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ont. Canada.

Johnson, M. G., and R. O. Brinkhurst. 1971. Associations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1683–1697.

Johnson, M. G., and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

Larsen, D. P., J. van Sickle, K. W. Malueg, and P. D. Smith. 1979. The effect of wastewater phosphorus removal on Shagawa Lake, Minnesota: phosphorus supplies, lake phosphorus and chlorophyll *a*. Water Res. 13: 1259–1272.

Larsen, D. P., and K. W. Malueg. 1980. Whatever became of Shagawa Lake?, p. 67–72. *In* Restoration of lakes and inland waters. EPA 440/5-81-010. U.S. Environmental Protection Agency, Washington, D.C.

McCombie, A. M. 1967. A recent study of the phytoplankton of the Bay of Quinte 1963–1964. Proc. Tenth Conf. Great Lakes Res. 37–62.

Millard, E. S. 1986. Seasonal trends in turnover times of orthophosphate in the Bay of Quinte, Lake Ontario, p. 91–99. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Millard, E. S., and M. G. Johnson. 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K. 1986. Total phosphorus loading to the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., and M. G. Johnson. 1986. Temperature and oxygen conditions and oxygen depletion in the Bay of Quinte, Lake Ontario, p. 40–49. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H., and E. C. Carney. 1979. The taxonomy of Bay of Quinte phytoplankton and the relative importance of common and rare taxa. Can. J. Bot. 57: 1591–1608.

1986. Nitrogen and phosphorus limitation to phytoplankton in the Bay of Quinte and implications for phosphorus loading controls, p. 139–144. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nordin, R. N. 1983. Changes in water quality of Skaha Lake, British Columbia, following reduction in phosphorus loading, p. 166–170. *In* Lake restoration, protection and management. EPA 440/5-83-001. U.S. Environmental Protection Agency, Washington, DC.

Owen, G. E. 1981. Point source nutrient inputs, p. 3–4. *In* "Project Quinte", Tenth Annual Report, 1981. Ontario Ministry of the Environment, Kingston, Ont.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC.) 195: 260–262.

Sorensen, T. 1948. A method for establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. K. Dansk. Vidensk. Selsk. Biol. Skrift. 5: 3–16.

Tucker, A. 1948. The phytoplankton of the Bay of Quinte. Trans. Am. Microsc. Soc. 67: 365–383.

Weiler, R. R. 1981. Chemistry of the North American Great Lakes. Verh. Int. Ver. Limnol. 21: 1681–1694.

Nutrient Loads and Budgets in the Bay of Quinte, Lake Ontario, 1965–81

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Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, P. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

The Bay of Quinte is a eutrophic bay at the eastern end of Lake Ontario where point-source phosphorus loadings were greatly reduced from 1978 onwards. Loadings and budgets for phosphorus, nitrogen, and chloride are presented for the period 1965–81. Whole-Bay and sectional budgets are examined, including the effect of exchange flows with Lake Ontario. By calculation, the role of internal loading is examined. The point-source phosphorus loadings have decreased dramatically, while nitrogen and chloride are little changed. The upper Bay budgets are dominated by internal loading, and a "catastrophe" model is proposed to describe its behaviour. In the upper Bay, there has been a shift from external to internal loading control. In the lower Bay, the budgets are dominated by a "nutrient pump," such as that seen in estuaries, driven by the exchange flows with Lake Ontario. Overall, while significant water quality improvements have been recorded, further improvements should be expected in the future as the internal loading dissipates and control is returned to external loading once again.

La baie de Quinte est un bassin eutrophe situé à l'extrémité est du lac Ontario où les charges locales en phosphore ont été fortement réduites depuis 1978. Le présent rapport porte sur les charges et les budgets du phosphore, de l'azote et du chlore pour la période 1965–81. On examine les budgets pour des parties et pour la totalité de la baie, y compris l'incidence des courants d'échange avec le lac Ontario. Le rôle de charge interne est aussi étudié à partir de calculs. Les charges locales en phosphore ont fortement diminué tandis que celles en azote et en chlore ont peu varié. Dans la partie supérieure de la baie, les budgets sont dominés par la charge interne; on présente un modèle de charge maximale pour décrire son comportement. À cet endroit, il y a aussi eu un déplacement du contrôle externe de la charge vers un contrôle interne. Dans la partie inférieure de la baie, une «pompe» de bioéléments, comme celle observée en estuaire, domine les budgets; elle est sous le contrôle des courants d'échange avec le lac Ontario. En général, quoiqu'on ait signalé des améliorations importantes de la qualité de l'eau, on peut s'attendre à d'autres changements futurs à mesure que la charge interne se dissipe et que la charge externe reprend le contrôle.

Introduction

Since the 1940's, the Bay of Quinte (BOQ) ecosystem has been degraded as a result of excessive nutrient loading. Its condition has been marked by noxious algal blooms and loss of significant fish habitat (Johnson and Owen 1971; McCombie 1967). Considerable changes in the warmwater fish community have been documented by Hurley and Christie (1977). The most recent change of note was the collapse of a large commercial and recreational walleye (*Stizostedion vitreum vitreum*) fishery at the end of the 1950's, a collapse which has been attributed to both direct and indirect effects of cultural eutrophication.

By the 1960's, the developed countries were beginning to address the problems associated with increasing nutrient loading of lake and rivers, as pointed out by Vollenweider (1968) and others. Johnson and Owen (1971) presented their 1968 phosphorus and nitrogen budgets of BOQ and thereby brought attention to its nutrient problems. Subsequently, plans were set to build improved phosphorus removal facilities at the main population centres on the Bay. They treated the Bay as a chain of five compartments, and serial transfers of water and nutrients were calculated. Their results showed that, while point-source inputs contributed only 40% of the absolute annual loading, the net loading, where displacement of nutrients due to river flows was allowed for, was dominated by the point-source inputs, i.e. the towns and cities on the shores of the Bay. The river inflows acted in general to dilute Bay waters.

The purpose of this study is to present estimates of the loadings and budgets of phosphorus (P), nitrogen (N), and chloride (Cl), a conservative ion, over the period 1965–81. We intend examining changes in the budgets in relation to changes in hydrology and point-source inputs. This approach will be applied on an annual and summer (May to September) basis to subsections of the Bay. This supports one objective of Project Quinte, which is to determine the relationship among point-source P control, runoff, hydrodynamics, sediment–nutrient–dynamics, and biota in regulating P concentrations in the Bay.

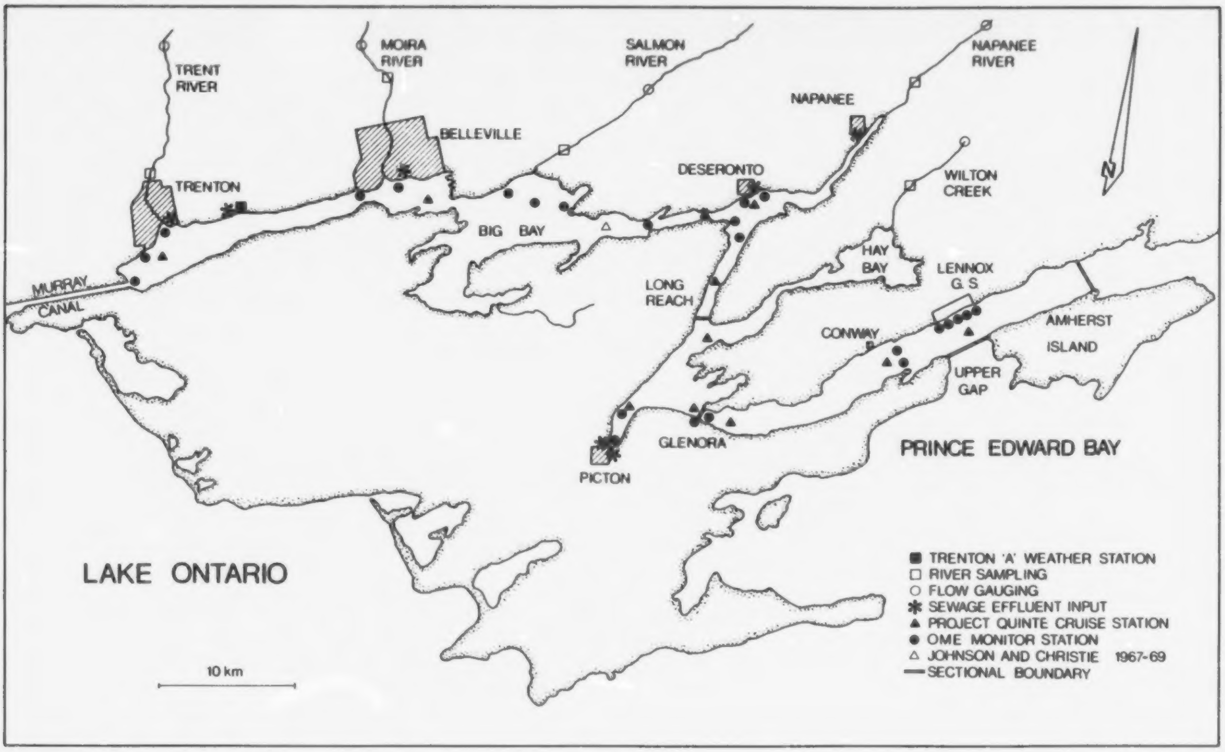

TRENT RIVER
MOIRA RIVER
SALMON RIVER
NAPANEE RIVER
NAPANEE
BELLEVILLE
TRENTON
DESERONTO
WILTON CREEK
N
MURRAY CANAL
BIG BAY
LONG REACH
HAY BAY
LENNOX G.S.
CONWAY
AMHERST ISLAND
UPPER GAP
GLENORA
PICTON
PRINCE EDWARD BAY
LAKE ONTARIO
10 km
■ TRENTON 'A' WEATHER STATION
□ RIVER SAMPLING
○ FLOW GAUGING
✱ SEWAGE EFFLUENT INPUT
▲ PROJECT QUINTE CRUISE STATION
● OME MONITOR STATION
△ JOHNSON AND CHRISTIE 1967-69
— SECTIONAL BOUNDARY

FIG. 1. Bay of Quinte showing the location of the sampling stations, the point sources, and the sectional boundaries.

The treatment of the Bay in sections is made necessary by the occurrence of significant water exchanges between the lower Bay (northeast of Glenora) and the outlet basin of Lake Ontario (Prince Edward Bay) at the upper gap (Fig. 1). Recent hydrodynamic studies (Freeman and Prinsenberg 1986; Prinsenberg 1978) have demonstrated the occurrence of upwelling in the basin in the triangle between Glenora, Picton, and the south end of Long Reach. During the summer when the waters of the Bay are thermally stratified, there is a substantial backflow of water, at depth, through the Glenora gap, which mixes with the outflow of the upper Bay below Long Reach. Further evidence indicates, at least in the summer, that water is always moving from Lake Ontario into the Bay through the upper gap and that the main outflow of BOQ is at the northeast end of Amherst Island. The exchange of BOQ and Lake Ontario waters can be estimated, as there is a large difference in the Cl concentrations of water from the two sources. The Cl budgets provide a means of examining this phenomenon and its effects on the nutrient and water budgets.

Materials and Methods

Morphometry and Drainage

Morphometric parameters were determined using maps published by the Canadian Hydrogaphic Service. A 0.56-m correction was used to adjust depths for the difference between the map datum and the long-term mean lake level at Kingston. For much of the analysis, we treated the Bay as a three-compartment system: upper, middle, and lower. The upper Bay consists of the area from Trenton, past Belleville through Big Bay, past Napanee down to the end of Long Reach (Fig. 1). Above this point, there was no evidence of incursions of high [Cl] waters, i.e. lower Bay water. The middle Bay consists of the area between the end of Long Reach, Picton, and Glenora plus Hay Bay, a shallow (1–2 m) expanse collecting the Wilton Creek drainage. The Glenora gap is one of the narrowest points on the Bay. The lower Bay consists of the area northeast of Glenora, past Conway and Lennox out to the marked boundaries (Fig. 1), the shallow sill at the upper gap, and the shallowest point halfway along Amherst Island. The lower Bay section is commonly known as Adolphus Reach. Hypsometric curves illustrate the wide range of topography from the large shallow expanse of the upper Bay to the fjord-like trough of the lower Bay (Fig. 2).

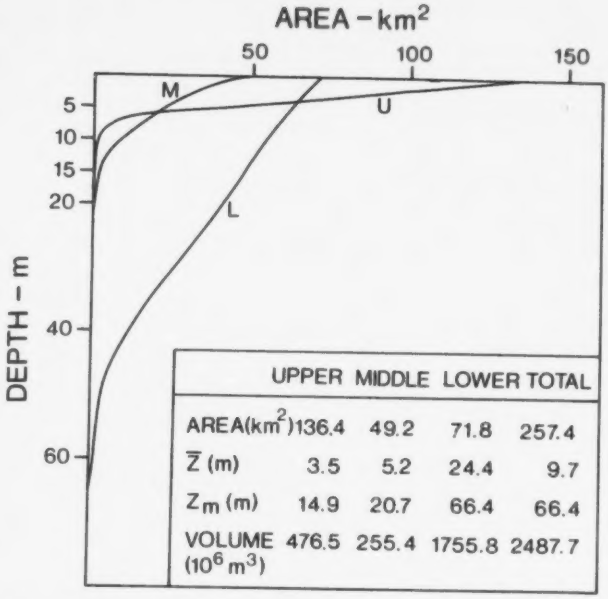
BOQ has a large drainage area (Table 1) with a ratio of land to bay area of 70:1 (Fig. 3). The area is almost equally divided between igneous and sedimentary rockforms (Fig. 3). The Trent River alone accounts for 67% of the drainage, with the Moira, Salmon, and Napanee rivers accounting for a further 26%. These rivers drain predominantly forested land with some pasture and cropland on the southern sedimentary areas. Wilton Creek and the many small drainage areas close to the Bay are mostly in agricultural use for crops, orchards, and pasture.

Water Budget

Nominal monthly water budgets were calculated for the three sections of BOQ using the following simple equation:

$$\text{Outflow} = \text{River inflow } (+\text{ above section outflow}) + \text{Precipitation} - \text{Evaporation} - \text{Volume change}$$

The Trent, Moira, Salmon, and Napanee rivers and Wilton Creek are gauged (Fig. 1) continuously by the Water Survey of Canada. Total river inflow from these sources was calculated by



	UPPER	MIDDLE	LOWER	TOTAL
AREA(km^2)	136.4	49.2	71.8	257.4
$\overline{Z}$ (m)	3.5	5.2	24.4	9.7
Z_m (m)	14.9	20.7	66.4	66.4
VOLUME (10^6 m^3)	476.5	255.4	1755.8	2487.7

FIG. 2. Hypsometric curves for the three Bay sections and the associated morphometric data.

prorating using drainage area ratios. For the miscellaneous drainage areas, the Wilton Creek flows were prorated rather than using an average of all gauged rivers, since the response of hydrographs to precipitation is more rapid in smaller drainages. The total river inflow to the upper Bay is equal to the sum of those from the Trent, Moira, Salmon, and Napanee rivers and 5.8 Wilton Creek equivalents. River inflow to the middle Bay is 3.1 Wilton Creek equivalents and that to the lower Bay is 0.7 equivalents.

Rain and snowfall onto the surface of the Bay was assumed to equal the measurements available at the Trenton A weather station (Fig. 1). BOQ is usually frozen over from the end of December until the beginning of April. Therefore, we assumed that the January to March snowfall accumulated on the ice and was released into the Bay at ice-out so the accumulations enter the budget calculations in April.

Given the large surface area of BOQ, particularly the large shallow area of the upper Bay, evaporation could not be ignored. However, it could not be calculated by the usual difference method of balancing inflow and outflow, since the outflow of the Bay cannot be measured directly. Meredith (1975) developed monthly regression equations to predict each of the main components, including evaporation of the water budgets of each of the Great Lakes. Those equations for evaporation were primarily linear functions of mean monthly air temperature and mean monthly surface water temperature. Using air temperature data from records of the Trenton A weather station and water temperatures summarized from regular measurements throughout the Bay, Meredith's evaporation equations for Lake Ontario were used to estimate the rates for the months April through December, when the Bay was ice free. Distinct rates were calculated for the three Bay sections, since surface water temperatures differed markedly.

Mean monthly surface water temperatures for the three Bay sections were not available for the whole period of study. However, mean monthly temperatures for the intake at the Belleville water filtration plant were available for the whole period, and simple regressions were used to estimate missing values.

Volume changes from month to month due to lake level changes were calculated using values for Kingston. Lake level changes in the BOQ reflect changes in the level of Lake Ontario, and there was no evidence that BOQ levels differ, even when inflows to the Bay are high.

Rivers Inputs

River inputs of P and N were previously reported by Minns and Johnson (1979), for the period 1965–74, for the Trent, Moira, Salmon, and Napanee rivers and Wilton Creek. The inputs were calculated using the rating curve technique adopted by Johnson and Owen (1971). Regressions were calculated for each river–year–substance combination with sufficient data using the following equation:

$$\log_e M = \log_e a + b \log_e Q$$

where M = daily substance export (kilograms per day), Q = daily flow (cubic metres per day), and a and b = regression coefficients.

Previously, Minns and Johnson (1979) used a combined estimate of b across years for each river–substance combination. When the analysis was extended to cover the period 1965–81, a different approach was used, which made the greatest use of data to estimate that year's export. For river–year–substance combinations with sufficient data and a regression result with a very high significance, the obtained regression equation was used. In cases where there were insufficient data, or the regression result was poor or insignificant, a common slope b from all other years was used to estimate a. For those river–year–substance combinations with no data at all, the overall regression for all data was used.

The regression equations were used to predict daily inputs from the five gauged drainages, suitably prorated. Inputs from the miscellaneous drainage areas (Fig. 3) were estimated by prorating Wilton Creek inputs. This procedure was justified on the basis of expected similarity of hydrographs and the similarity of land use (Table 1).

Atmospheric Loading

Monthly atmospheric loadings of P, N, and Cl have been measured at Trenton and Kingston airport weather stations since 1969 by the Water Quality Branch, Inland Waters Directorate, Environment Canada. Methods and procedures have been described by Shiomi and Kuntz (1973) and by Kuntz (1980).

At various times, different collectors have been used (Table 2). The samples are mostly monthly collections. At the time of this analysis, data up to 1 April 1981 were available. Deposition rates for total Kjeldahl nitrogen (TKN), nitrate + nitrate (NO_3 + NO_2), total P, and Cl were analyzed. Preliminary analysis indicated no differences between stations or sampler type, so all data were pooled. There were a few extreme values in the data sets for each variable. These values were identified as outliers using the 95% confidence interval on $\log_e$-transformed data and were eliminated from further analysis. The rejected values were considered to represent contaminated samples (Table 3).

The monthly loading rates were analyzed for secular and seasonal trends as well as for a relationship with variables such as monthly precipitation at Trenton and mean monthly air temperature.

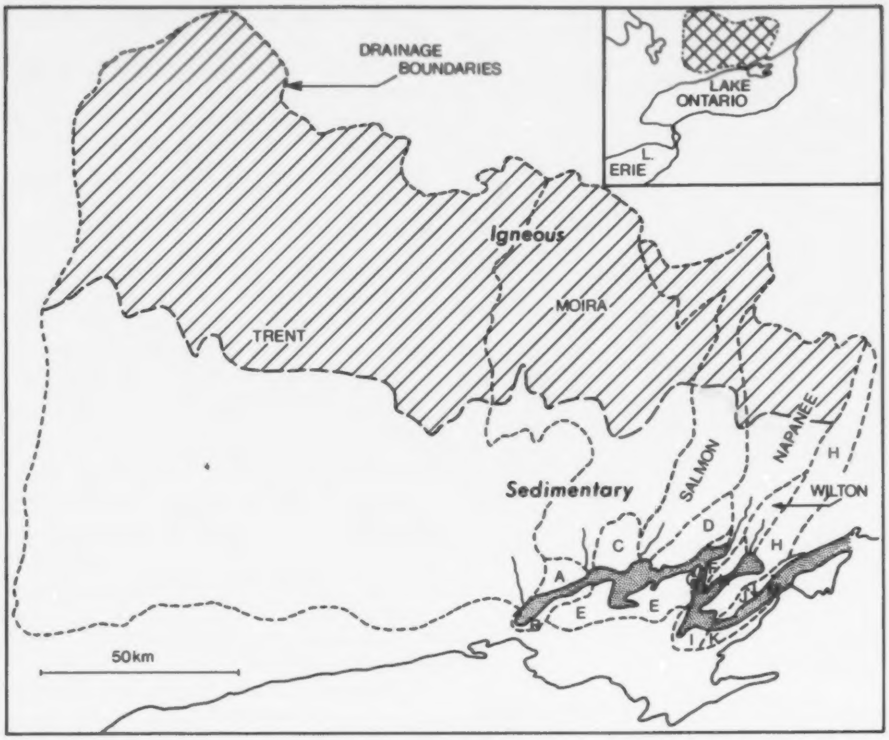


FIG. 3. Drainage basin of the Bay of Quinte with the drainages of the major rivers and the many miscellaneous areas delimited (crosshatching for igneous rockforms).

TABLE 1. Drainage areas and their land use around the Bay of Quinte.[a]

	Drainage[b]	Area (km²)	% urban	% agriculture	% forest	% marsh/swamp
Upper Bay	Trent R.	12548.7	0.9	36.1	59.7	1.9
	Misc. A	114.5	11.2	68.9	17.1	—
	Misc. B	21.8	—	74.5	21.4	4.2
	Moira R.	2737.2	0.6	26.6	69.4	2.9
	Salmon R.	897.5	0.4	31.9	62.7	3.1
	Misc. C	110.0	7.2	69.9	19.5	—
	Misc. D	215.6	1.1	83.5	14.3	1.2
	Misc. E	231.8	0.1	63.1	28.0	8.4
	Napanee R.	787.0	1.1	40.5	56.2	2.0
	Misc. F	28.1				
	Misc. G	12.6	—	67.4	28.2	4.4
Middle Bay	Wilton Cr.	127.4	0.3	74.5	23.3	2.0
	Misc. H	220.0				
	Misc. I	44.8	8.7	64.7	25.8	—
Lower Bay	Misc. J	22.9	—	82.6	17.4	—
	Misc. K	34.3	—	71.3	22.6	1.4
	Misc. L	22.0	—	82.6	17.4	—
	Misc. M	5.5	—	77.9	19.3	2.7
Total		18181.6	1.0	37.1	58.7	3.3

[a] Derived from Lands Management Information Systems/Lands Directorate, Environment Canada.

[b] Miscellaneous drainages are shown on Fig. 3.

Point-Source Inputs

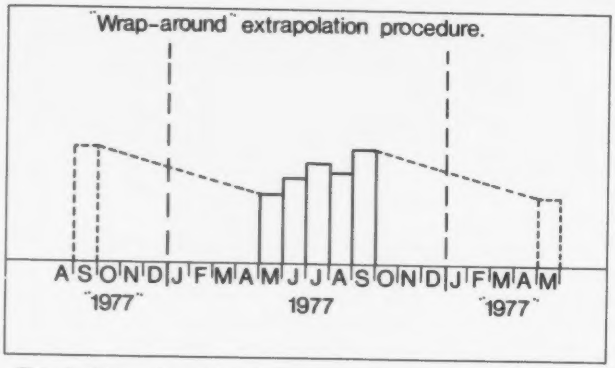
There are five municipal sources of nutrients, situated at Trenton, Belleville, Deseronto, Napanee, and Picton. Inputs from two Canadian Forces bases at Trenton and Picton were also considered. Sewage treatment plant loadings were originally calculated from mean annual measured flows through the plants and the mean annual final effluent concentrations derived from six to forty-one 24-h composite samples. The frequency of effluent sampling for most plants and years has been less than 12

TABLE 2. Disposition of precipitation collectors used by Environment Canada at Trenton and Kingston.

Location	Code	Type	Sampling area (m^2)	Time span
Trenton	HK01	Bulk	0.0112	Aug. 1969 – Aug. 1977
	HK02	Bulk	0.0506	Dec. 1972 – Present
	HK07	Wet only	0.0314	Aug. 1977 – Present
Kingston	HM01	Bulk	0.0112	July 1969 – Present

TABLE 3. Mean and standard deviation of source atmospheric loading data.

Substance	*N*	Mean	SD	No. rejected at 95% level	Detransformed mean ($mg \cdot m^{-2} \cdot d^{-1}$)
TKN	217	0.251	0.699	10	1.285
$NO_2 + NO_3$	313	0.403	0.580	14	1.496
P	315	−3.279	1.317	13	0.038
Cl	309	0.521	0.939	12	1.684


"Wrap-around" extrapolation procedure.
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"1977"
1977
"1977"

FIG. 4. Illustration of the "wrap-around" extrapolation procedure.

times annually, except for Trenton, where between 12 and 26 samples were taken in the years 1969–77. In 1976, sampling was generally increased for the purposes of monitoring and operational control as P removal was implemented. Since 1976, loading calculations have been done on a monthly basis, since in some years some plants show considerable seasonal variation. The point-source loadings estimated in the above manner compared well with per capita estimates (Minns 1986).

Loadings due to bypassed sewage were not known. Overall, it has been estimated that bypass loading was about 10% of total sewage loading. Since these bypass releases occur in seasons of high river flow, we increased the estimates by 10% and apply the additional loading to the months of March and April (2.5% each) and November, December, and January (1.7% each) when river flows are highest.

Loadings in the Trenton area were augmented by inputs from two industrial sources. In Deseronto, loadings were augmented by seasonal inputs from a vegetable processing plant. The processing season runs from June to November, and for the remainder of the year loadings were negligible. A treatment plant was installed in 1973 which reduced loadings early in the season, but the plant was overloaded in August and September. Changes in inputs from the Canadian Forces base at Trenton have generally paralleled those from the city. Inputs from the base at Picton ceased when the base closed in 1969.

Bay Substance Concentrations

All available measurements of P, N, and Cl in the Bay were assembled. The analyses were all performed by the Ontario Ministry of the Environment (OME) either as a result of monitoring cruises or as part of Project Quinte activities, using methods described elsewhere (Ontario Ministry of the Environment 1975).

In the years 1967–69, sampling was carried out monthly or twice monthly during the ice-free season (Johnson and Owen 1971; Christie 1973a, 1973b). Most data were obtained for stations at Big Bay, Glenora, and Conway (Fig. 1) and consisted of both depth-integrated samples and point samples at depth.

In the years 1967–69, 1972, and 1974, OME conducted monitoring cruises through BOQ at 18 stations, three to five times in each year. Sampling at each station consisted of a surface-integrated sample and point samples at 10-m intervals on three successive days.

Since Project Quinte began in 1972, a weekly cruise has been conducted at seven stations (eight, 1975–78; five, 1979–81) throughout the Bay (Fig. 1) from the end of April or beginning of May until the beginning of October. In addition, in some years, samples were collected at connecting channels in the Bay at Belleville, Deseronto, and Long Reach. A few samples were collected in the winter months, but only rarely because of ice-related logistic problems. The samples at each station consisted of an integrated sample of the euphotic zone, i.e. twice the Secchi depth, and a point sample taken 1 m from the bottom. After 1977, midwater point samples were taken at the Glenora and Conway stations.

Samples taken during the period 1972–77 were rarely analyzed for Cl, but always for sodium (Na). Since there was a good correlation between these two conservative ions, we converted Na values to Cl equivalents. In 1978, all samples from Project Quinte cruises were analyzed for both ions and a regression equation was calculated:

$$Cl\ (mg \cdot L^{-1}) = -1.695 + 2.1214\ Na\ (mg \cdot L^{-1})$$

$$N = 466, r = 0.942.$$

This equation was used for the conversion.

Statistical analysis of Project Quinte water quality data provided the basis for the reduction in station number from 8 to 5 after the 1978 field season, and provided a rationale for treating the Bay in three sections. The upper Bay stations at Trenton, Belleville, and Napanee were generally similar, as were the stations at Conway and Lennox. From Napanee to Conway, the stations at Hay Bay, Picton, and Glenora followed a steady trend, although Picton was more similar to Hay Bay and Glenora

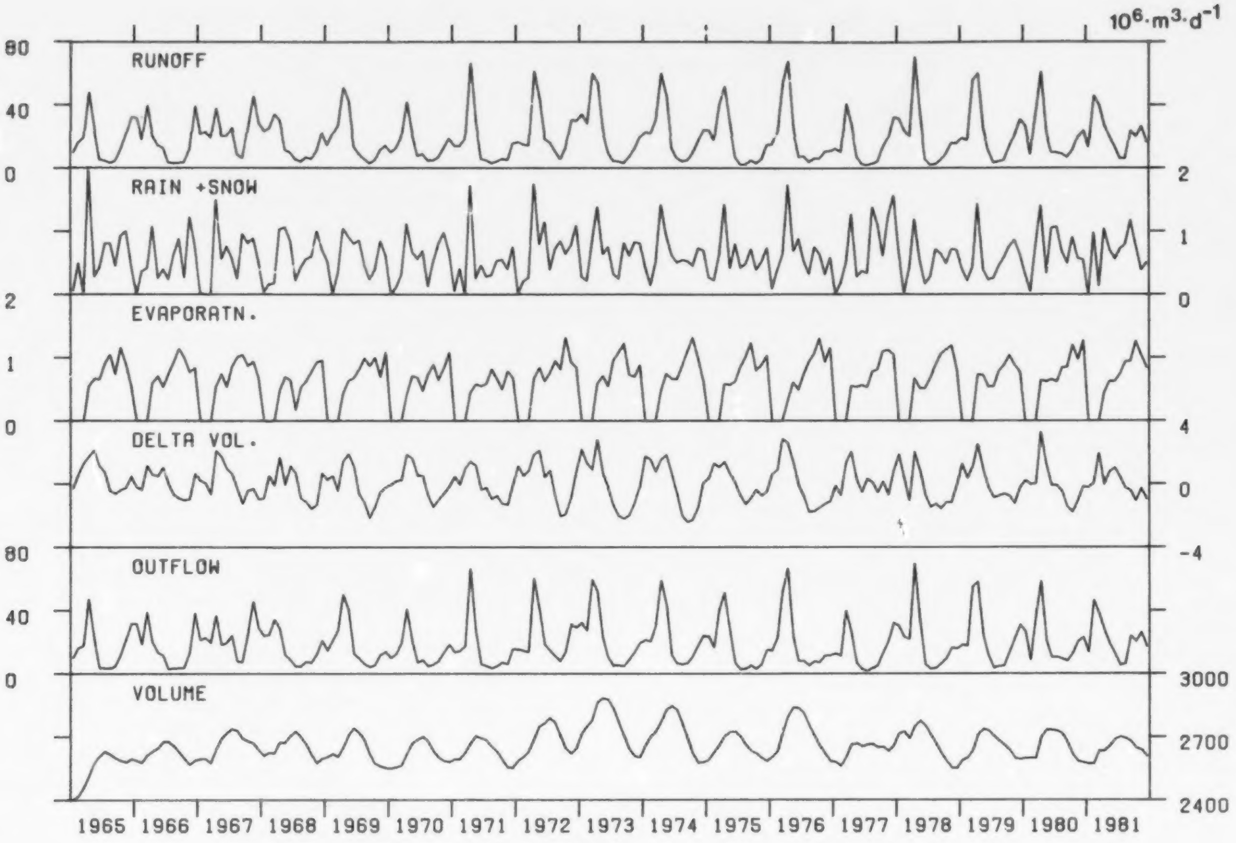


FIG. 5. Monthly water budget of the Bay of Quinte by component, 1965–81.

lay midway between those stations and Conway. Analysis of surface data also indicated that data collected within calendar months were relatively homogeneous.

On the basis of these results, the data on P, N, and Cl were summarized by computing time-weighted depth-integrated monthly means. The upper Bay was summarized as a single unit and then the stations in the Deseronto and Napanee area were taken to represent the effluent concentration of the upper Bay. The middle Bay was composed of two layers, surface (0–5 m) and bottom (>5 m), drawing on data from the Picton – Hay Bay area stations. The lower Bay was also composed of two layers, and three sets of means were calculated: (i) data from the immediate vicinity of the Glenora gap defined the boundary between the middle and lower Bay sections; (ii) data from all lower Bay stations defined the lower Bay section concentrations; and (iii) data from the Conway–Lennox area defined concentrations at the outer boundary of the Bay.

Mean monthly concentrations were available, in most instances, only for the period April to October, and consequently, a method of extrapolation to the winter months was sought. For P, N, and Cl, good correlations were obtained between mean monthly concentrations and mean monthly sectional outflow from the water budget for all 10 stations. However, when extrapolated to winter months when flows were generally much higher, the values predicted appeared ridiculous. Consequently, an interpolation method was used. Each year was assumed to "wrap around" on itself whereby each December followed its January, and values were then interpolated linearly (Fig. 4). The few data values available in the winter do not refute this assumption. An alternative method would have involved using previous and following years' data. This would not have produced appreciably different results, but at the start and end of groups of years a variant method would still have been necessary.

Chloride data from several stations in the outlet basin of Lake Ontario were used to define the source concentration for any water budget adjustments based on Cl imbalances. Available data were compiled from the files of the Water Quality Branch, Inland Waters Directorate, Environment Canada. All values in any month were pooled to give a mean monthly value. There was a definite secular trend in Cl levels, which fit a simple quadratic equation using year as an independent variable:

$$\mathrm{Cl}\,(\mathrm{mg\cdot L^{-1}}) = 25.24 + 0.5952\,(\mathrm{Year} - 1964) - 0.03254\,(\mathrm{Year} - 1964)^2$$

$$N = 73,\ r = 0.72,\ F = 15.64 \text{ on } 2{,}70 \text{ df.}$$

This regression was used to estimate annual [Cl] values for the period 1965–81. There were insufficient data to define boundary conditions for P and N in the outlet basin. The few P values available were slightly lower than those found in the Conway–Lennox region of the Bay, as might be expected.

Seasonal and secular trends in nutrients and other parameters throughout BOQ are reviewed elsewhere by Robinson (1986). Most of the waters of BOQ are well mixed at all times and consequently the limited numbers of stations and sampling depths are considered adequate for estimating the nutrient content and output of Bay sections.

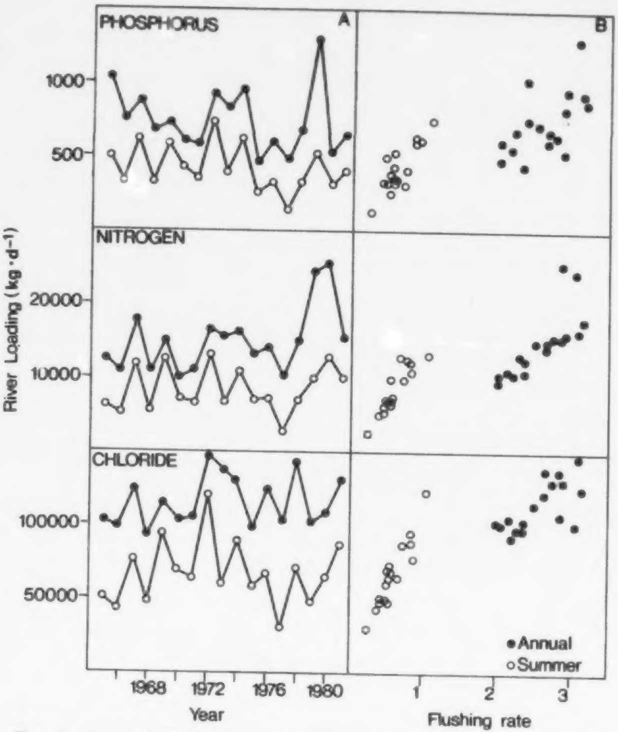


FIG. 6. Trends in the annual and summer river loadings of P, N, and Cl with (A) time and (B) uncorrected annual and summer Bay flushing rates.

Results

Water Budget

These budgets were calculated as reference points without any correction for exchanges with Lake Ontario. River flows dominated the budget of BOQ (Fig. 5) on an annual basis. There were pronounced seasonal differences, with flow rates at their lowest in the summer period. Peak flows generally occurred in the March to April period. Flushing rates highlight the summer versus the rest of the year differences (Table 4). The whole bay may be flushed 2.00 to 3.20 times a year, but only 0.25 to 1.03 times per summer of 153 d (1 May to 30 September). The Bay sections exhibit a range of flushing regimes, with the middle Bay being the most dynamic.

River Inputs

River inputs fluctuated from year to year along with variation in runoff (Fig. 6). Both N and Cl loadings appeared to increase slightly over the period, while P loading decreased. Mean summer inputs were much lower than annual inputs. Although the summer represents 41% of the calendar year, P input varied from 11.9 to 35.4%, N from 10.6 to 35.3%, and Cl from 12.6 to 34.8%. Loading and flushing rate per summer or year (proportional to runoff) were strongly related (Fig. 6) although most weakly for P. Also, mean summer input concentrations were higher than mean annual levels.

Atmospheric Loading

Analysis of variance for monthly variation showed that P, TKN, and $NO_2 + NO_3$ showed effects, in that order, while Cl showed no effect (Table 5). TKN and P loading rates are higher in the summer months. $NO_2 + NO_3$ show significant variability from month to month, but with no consistent trend.

Loading rates were then regressed with mean monthly air temperature, rainfall, and snowfall, as well as with year, to look for secular trends. The following significant regressions were obtained:

$$\begin{aligned}
\log_e(\mathrm{TKN}) &= -0.2509 + 5.726\ \mathrm{Rain} \\
&\quad + 0.0161\ \mathrm{Temperature} \\
r &= 0.474,\ F = 29.59 \text{ on } 2{,}204 \text{ df} \\
\log_e(NO_2 + NO_3) &= 1.3036 + 5.896\ \mathrm{Rain} \\
&\quad - 0.0160\ \mathrm{Year} \\
r &= 0.470,\ F = 42.02 \text{ on } 2{,}296 \text{ df} \\
\log_e(\mathrm{P}) &= -3.740 + 0.0544\ \mathrm{Temperature} \\
r &= 0.484,\ F = 91.87 \text{ on } 1{,}300 \text{ df.}
\end{aligned}$$

With Cl, no significant predictive equations were obtained.

The monthly inputs to BOQ were calculated for P and N ($TKN + NO_2 + NO_3$) using the regressions above, while a fixed value was used for Cl based on the log-mean ($1.615\ mg \cdot m^{-2} \cdot d^{-1}$). Use of fixed values for P and N loading would not have altered the overall loadings very much, since atmospheric loading is only a small proportion.

Inputs of P and N are higher in the summer (Fig. 7) although overall inputs are much lower than river inputs.

Point-Source Inputs

There have been significant changes in P loading from point-sources over the period 1965–81 (Fig. 8). Before major improvements in sewage treatment were implemented 1978, there had been a decline in inputs from over 300 $kg \cdot d^{-1}$ down to about 200 $kg \cdot d^{-1}$, a 33% reduction. Once the new treatment plants were operational, a further reduction was achieved with a drop from 200 $kg \cdot d^{-1}$ down to an average for 1978–81 of 84 $kg \cdot d^{-1}$. The improvements prior to 1978 were due to two things, a general reduction of the level of phosphates in household detergents and an upgrading of existing sewage treatment facilities. Further, since 1978, summer loadings have been reduced by the use of chemically enhanced P removal.

Nitrogen inputs from point-sources remained steady over the whole period. Chloride inputs increased during the early 1970's and have been relatively level since.

Uncorrected Whole-Bay Budgets

We constructed uncorrected budgets, i.e. without the incursions of Lake Ontario waters (Table 6). As expected, the Cl budgets exhibited high negative retention (output > input). Nitrogen and P budgets indicated a moderate to high retention, typical for temperate lakes (Nurnberg 1984).

Total annual external P loading averaged 1.4 $g \cdot m^{-2} \cdot yr^{-1}$ prior to 1978 and 1.25 since, 88% of former levels. Summer loadings averaged 2.7 $mg \cdot m^{-2} \cdot d^{-1}$ prior to 1978 and 1.9 since, 69% of former levels. Nitrogen and Cl loads fluctuated with changes in runoff. Nitrogen loading ranged between 49.7 and 106.2 $mg \cdot m^{-2} \cdot d^{-1}$ annually and 17.3 and 59.4 in the summer.

Annual point-source P inputs contributed 16–38% of the total external load up to 1977 and 5–14% since. The corresponding summer values were 20–54 and 9–18%. This contribution was

TABLE 4. Whole-Bay and sectional flushing rates, uncorrected and corrected for backflows from Lake Ontario.[a]

Year	Uncorrected				Corrected		
	Upper	Middle	Lower	Whole	Middle	Lower	Whole
Annual							
1965	11.9	22.4	3.3	2.3	—	—	—
1966	11.0	21.7	3.4	2.3	—	—	—
1967	14.6	29.1	4.7	3.2	84.2	16.4	11.6
1968	9.9	20.1	3.2	2.2	50.1	8.5	6.0
1969	11.4	22.9	3.7	2.5	99.0	8.4	5.9
1970	9.2	18.2	2.9	2.0	—	—	—
1971	9.8	19.6	3.1	2.1	—	—	—
1972	13.9	28.1	4.6	3.1	219.5	9.5	6.7
1973	12.3	25.4	4.3	2.8	346.8	11.5	8.1
1974	12.8	26.0	4.3	2.9	81.6	12.9	9.1
1975	10.3	20.9	3.4	2.3	97.4	9.2	6.5
1976	11.6	23.7	3.9	2.6	54.0	9.6	6.8
1977	9.2	18.5	2.9	2.0	131.4	7.7	5.4
1978	11.8	23.9	3.9	2.6	55.6	19.6	13.8
1979	13.8	27.8	4.4	3.0	312.4	16.7	11.8
1980	12.9	25.9	4.1	2.8	236.6	15.8	11.2
1981	13.1	25.5	4.0	2.7	101.5	16.5	11.6
Summer							
1965	2.28	4.36	0.66	0.45	—	—	—
1966	1.94	3.82	0.61	0.41	—	—	—
1967	4.03	8.04	1.31	0.88	16.41	4.02	2.84
1968	1.89	3.94	0.65	0.44	6.81	4.58	3.23
1969	3.71	7.54	1.25	0.84	18.90	4.46	3.15
1970	2.49	4.97	0.80	0.54	—	—	—
1971	2.42	4.86	0.79	0.54	—	—	—
1972	4.59	9.39	1.58	1.05	19.18	4.20	2.96
1973	2.11	4.47	0.80	0.52	23.14	3.58	2.53
1974	3.47	7.22	1.26	0.83	20.63	6.16	4.35
1975	2.28	4.62	0.77	0.51	21.42	3.81	2.67
1976	2.36	4.93	0.86	0.57	19.62	5.63	3.97
1977	0.98	2.02	0.33	0.23	12.16	2.11	1.49
1978	2.47	5.09	0.87	0.58	15.00	6.36	4.49
1979	2.42	4.95	0.82	0.55	22.48	7.17	5.06
1980	2.95	6.10	1.02	0.68	22.32	6.87	4.85
1981	3.33	6.58	1.06	0.72	19.36	5.17	3.65

[a] Times per year and times per summer (May to September inclusive).

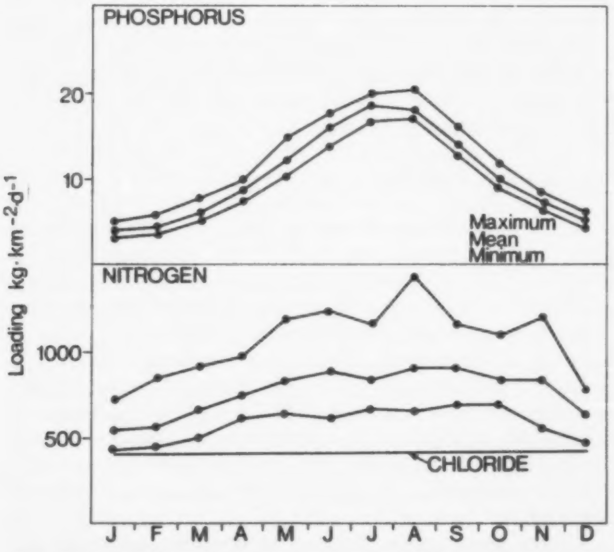


FIG. 7. Seasonal trend in the atmospheric loadings of P and N and mean loading of Cl.

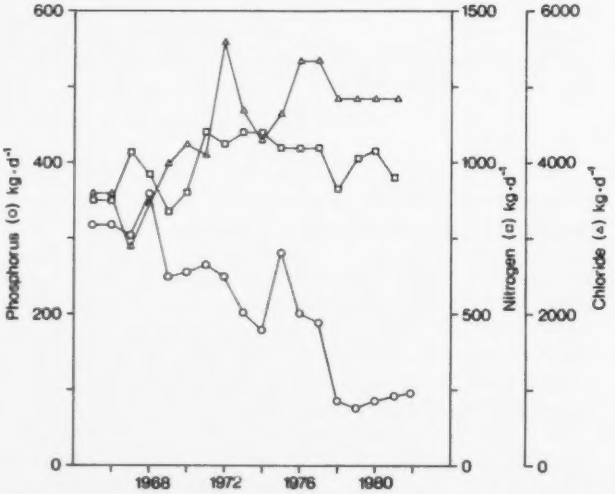


FIG. 8. Annual mean point-source loadings of P (○), N (□), and Cl (Δ) to the Bay of Quinte, 1965–81.

TABLE 5. Analysis of variance for seasonal effects on monthly atmospheric loading rates (**significant at $p < 0.005$; NS, not significant at $p < 0.10$).

Substance	df	Error MS	Treatment MS	Ratio
TKN	11,195	0.2864	1.3084	4.57**
$NO_2 + NO_3$	11,287	0.1596	0.4731	2.96**
P	11,301	0.9494	9.5391	10.05**
Cl	11,296	0.6555	0.7645	1.17 NS

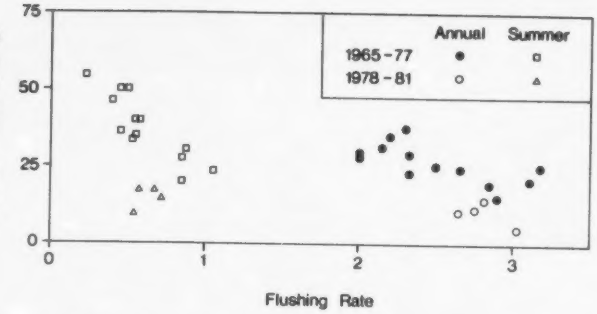


FIG. 9. Relationship between point-source loading as a percentage of total external loading and the uncorrected Bay flushing rates.

inversely related to the uncorrected flushing rate, which is proportional to runoff (Fig. 9). Point-source N inputs contributed 6–22% of the total in the summer and 4–9% annually. The bulk of Cl loading came from the rivers.

Corrected Bay Budgets

The Cl imbalances in the middle and lower Bay sections (Fig. 10) were used to estimate the exchange backflows from Lake Ontario. Simple mass balance equations were used rather than advection–diffusion equations. For each section, the output of Cl was set equal to inputs plus the change in storage, as follows:

$$(1)\quad (Q_M + Q_1)[\mathrm{Cl}]_M = E_M + Q_1[\mathrm{Cl}]_L + \Delta S_M$$

$$(2)\quad (Q_L + Q_1 + Q_2)[\mathrm{Cl}]_L = E_L + Q_2[\mathrm{Cl}]_O + Q_1[\mathrm{Cl}]_M + \Delta S_L .$$

These can be rearranged:

$$(3)\quad Q_1 = (Q_M[\mathrm{Cl}]_M - \Delta S_M - E_M)/([\mathrm{Cl}]_L - [\mathrm{Cl}]_M)$$

$$(4)\quad Q_2 = (Q_L[\mathrm{Cl}]_L - \Delta S_L - E_L + Q_1([\mathrm{Cl}]_L - [\mathrm{Cl}]_M)/([\mathrm{Cl}]_O - [\mathrm{Cl}]_L)$$

where Q_M and Q_L = net middle and lower Bay outflows, Q_1 and Q_2 = middle/lower and lower/Lake Ontario exchange backflows, $[\mathrm{Cl}]_M$, $[\mathrm{Cl}]_L$, and $[\mathrm{Cl}]_O$ = middle and lower Bay outflow and Lake Ontario Cl concentrations, E_M and E_L = upstream loading to middle and lower Bay sections, and ΔS_M and ΔS_L = section changes in store of Cl, middle and lower Bay. Equation (3) is solved first and then (4) month by month, taking into account storage changes, upstream inputs, and net outflow. The backflows Q_1 and Q_2 were then used to correct the P and N sectional budgets. The flows were considerable compared with net Bay outflow (Q_L) (Table 7).

To do the calculation, it was necessary to have monthly Lake Ontario $[\mathrm{P}]_O$ and $[\mathrm{N}]_O$ values. There were incomplete data for $[\mathrm{P}]_O$ and only a few values for $[\mathrm{N}]_O$. To work around this problem, one solution would have been to assume that $[\mathrm{P}]_O = [\mathrm{P}]_L$ and $[\mathrm{N}]_O = [\mathrm{N}]_L$. However, this leads to backflow loading and retention being overestimated. Another approach, which we adopted, involved the assumption that there is a fixed relationship between lower Bay and Lake Ontario nutrient concentrations. From summer surveys on Lake Ontario between 1969 and 1981, there were 29 mo in which there were $[\mathrm{P}]_O$ values for the outlet basin. Lake Ontario $[\mathrm{P}]_O$ was on average $3\ \mu g \cdot L^{-1}$ less than the lower Bay outlet $[\mathrm{P}]_L$, although this was a highly variable relationship. As a minimum correction for the whole Bay and sectional budgets, we assumed the following:

$$(5)\quad [\mathrm{P}]_O = [\mathrm{P}]_L - 0.003\ \mathrm{mg \cdot L^{-1}}$$

$$(6)\quad [\mathrm{N}]_O = [\mathrm{N}]_L \cdot ([P]_L - 0.003)/[\mathrm{P}]L .$$

This has the effect of assuming that (i) changes in the lower bay have been mirrored by changes in Lake Ontario (a reasonable assumption given widespread efforts to reduce P loading), (ii) Lake Ontario backflow always displaces higher concentration water, thereby reducing retention, and (iii) N : P ratios are similar in the lower Bay and Lake Ontario. The assumptions made here are an important contributor to the overall uncertainty in these analyses. It is extremely unlikely that Lake Ontario nutrient levels were equal or greater than lower Bay ones. If Lake Ontario nutrient levels were lower than assumed here, there would be a shift from positive toward zero or negative retention values, enlarging the role of internal loading, i.e. sediment reflux.

The corrected whole-Bay budget for P and N (Table 7) illustrate the importance of the Lake Ontario backflow. The backflows (Q_1, Q_2) were generally of the same order as the net outflow (Q_L). Total loads of P and N were greatly increased and retention values were much lower.

The Lake Ontario backflow only affects the middle and lower Bay sections. Lower Bay conditions were controlled equally by upper Bay transfers and backflow. Any response to reduced P loading was most likely to be seen in the upper Bay budgets.

Sectional Budgets

The same correction method was used for sectional budgets with the addition of two compartment backflows. There was a backflow from the lower to the middle Bay and a backflow from Lake Ontario to the lower Bay (Fig. 10). In addition, we made calculations, separating sedimentation and sediment release (reflux) of nutrients.

Sediment reflux rates were calculated by estimating sedimentation, allowing for storage changes, and then forcing monthly budgets to balance. Charlton (1975) reported P sedimentation rates, corrected for resuspension, in limnocorrals sited in BOQ near Napanee. He found an average P loss of $2.9\% \cdot d^{-1}$ in a 4-m layer. This result can be used to estimate a mean sinking rate of $0.115\ m \cdot d^{-1}$ for total P. This value compares with results obtained by Johnson and Brinkhurst (1971) and C. K. Minns (unpubl. results) (Table 8). The former results were not corrected for resuspension, while the latter were. The sinking rates calculated from these data straddle the rate obtained by Charlton. Since Charlton's sinking rate was obtained under controlled conditions, we decided to adopt that rate for calculations. Since sedimentation is the result of material "sinking" or settling out of the water column, it is more logical to use a fixed sinking rate for all locations than to use a fixed loss coefficient. Fixed sinking rates are a central feature of general nutrient budget models (Dillon 1974; Chapra 1982).

The uncorrected Cl budgets indicate the extent of the flow

TABLE 6. Loadings ($kg \cdot km^2 \cdot d^{-1} = mg \cdot m^{-2} \cdot d^{-1}$) and retention values for P, N, and Cl in the whole Bay of Quinte, 1965–81, uncorrected for Lake Ontario backflows.

	P		N		Cl	
	Load	% retention	Load	% retention	Load	% retention
Annual						
1965	5.3	—	54.8	—	1006.4	—
1966	4.2	—	48.1	—	1030.5	—
1967	4.6	39.0	76.9	22.4	1743.9	−247.6
1968	4.1	39.6	48.7	24.6	976.4	−160.2
1969	3.8	33.1	64.9	39.5	1072.2	−131.0
1970	3.4	—	44.7	—	923.0	—
1971	3.3	—	49.7	—	962.2	—
1972	4.6	47.8	70.8	39.7	1327.8	−122.1
1973	4.0	26.6	68.3	27.0	1622.2	−192.9
1974	4.4	51.6	70.1	17.2	1424.5	−171.1
1975	2.9	51.5	58.3	46.0	1174.0	−191.4
1976	3.2	45.2	61.9	30.7	1278.2	−154.8
1977	2.6	51.5	46.6	39.4	1122.9	−166.2
1978	3.0	50.8	63.9	31.2	1418.5	−147.2
1979	5.4	70.6	101.6	55.5	1611.6	−288.0
1980	2.4	30.3	106.2	57.5	1549.5	−250.7
1981	2.9	31.9	66.4	34.4	1642.1	−211.9
Summer						
1965	3.2	—	30.5	—	213.4	—
1966	2.5	—	26.3	—	184.0	—
1967	3.6	20.2	55.4	25.2	314.0	−220.8
1968	2.6	49.0	27.2	42.8	204.4	−184.7
1969	3.3	52.7	55.9	42.7	386.8	−126.5
1970	2.6	—	34.0	—	285.7	—
1971	2.4	—	31.3	—	263.6	—
1972	3.9	49.6	59.4	39.1	498.4	−97.3
1973	2.2	60.2	32.2	48.4	256.1	−173.4
1974	3.2	55.1	49.6	43.8	364.8	−169.4
1975	2.1	67.3	33.6	51.2	215.0	−141.0
1976	2.1	65.3	34.9	49.7	285.9	−198.8
1977	1.3	77.3	17.3	59.2	140.7	−138.1
1978	1.6	59.1	33.2	27.3	304.6	−113.8
1979	2.4	69.8	44.7	55.2	209.1	−223.9
1980	1.5	24.6	57.3	56.3	269.8	−240.9
1981	2.0	39.1	45.2	40.9	357.9	−188.7

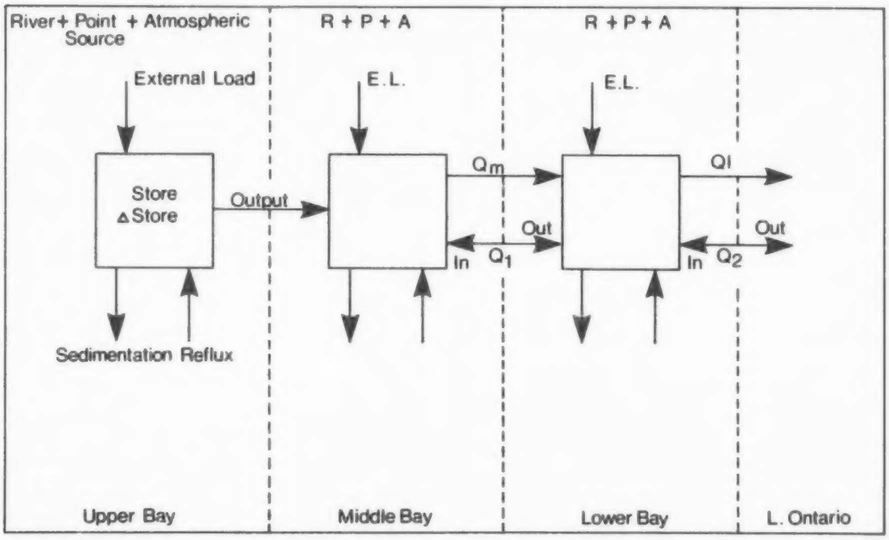

River+ Point + Atmospheric Source
R + P + A
R + P + A
External Load
E.L.
E.L.
Store
ΔStore
Output
Qm
Out
In
Q1
Ql
Out
In
Q2
Sedimentation Reflux
Upper Bay
Middle Bay
Lower Bay
L. Ontario

FIG. 10. Conceptual model of sectional budgets for the Bay of Quinte.

TABLE 7. Calculated mean annual and summer uncorrected Bay outflows (Q_L, $10^6\ m^3 \cdot d^{-1}$), exchange backflows from Lake Ontario (Q_1, Q_2, $10^6\ m^3 \cdot d^{-1}$), and corrected whole Bay nutrient budgets ($mg \cdot m^{-2} \cdot d^{-1}$), 1967–81.

Year	Net Bay Outflow (Q_L)	Exchange backflow: Middle lower (Q_1)	Exchange backflow: Lower Lake Ontario (Q_2)	P: Load	P: % retention	N: Load	N: % retention
Annual							
1967	23.1	43.3	57.9	9.6	15.0	177.4	2.7
1968	15.8	23.2	25.7	6.1	24.2	75.3	9.0
1969	18.1	58.9	23.0	5.8	24.5	88.4	24.1
1972	22.7	149.6	24.6	6.0	33.2	95.2	26.2
1973	21.7	267.7	35.9	7.9	8.0	132.0	8.1
1974	21.5	43.6	42.3	6.3	32.2	115.3	0.3
1975	16.7	59.8	28.7	4.6	31.4	91.7	23.8
1976	19.7	24.7	28.3	4.8	29.2	93.7	12.1
1977	14.5	87.9	23.3	4.4	25.3	86.2	13.7
1978	19.6	25.4	76.5	4.7	27.9	106.9	6.1
1979	22.1	221.4	60.2	7.9	44.5	166.4	25.6
1980	20.4	161.5	57.4	5.1	2.4	179.4	24.8
1981	19.8	59.2	61.8	8.0	−0.9	182.4	2.2
Mean	19.7	94.3	42.0	6.2	22.8	122.4	13.7
Summer							
1967	15.7	16.4	32.3	6.3	3.9	98.1	10.3
1968	7.6	5.5	46.2	4.5	20.1	49.0	15.9
1969	14.7	21.9	38.0	4.6	41.9	73.1	25.5
1972	18.9	19.7	31.6	4.6	37.7	74.0	24.0
1973	9.5	37.8	33.6	3.3	39.5	52.3	28.6
1974	15.0	27.3	59.0	4.3	36.7	71.4	24.8
1975	9.0	31.9	36.4	2.5	55.4	43.1	37.4
1976	10.2	29.8	57.3	3.8	38.7	69.9	21.4
1977	3.8	19.2	21.2	2.0	52.0	32.3	28.7
1978	10.1	19.2	65.3	2.1	43.5	46.6	7.9
1979	9.7	33.9	75.3	3.2	47.9	67.3	29.6
1980	12.0	31.7	70.1	3.2	−3.7	99.5	24.9
1981	12.5	24.6	48.8	4.7	0.1	111.6	6.3
Mean	10.7	24.5	47.3	3.8	31.8	68.3	22.3

TABLE 8. Sedimentation and sinking rates in the Bay of Quinte.

Location	Depth (m)	Year	Sedimentation (% $P \cdot d^{-1}$)	Sinking rate ($m \cdot d^{-1}$)[b]	Source
Glenora	20.0	1967	0.87	0.174	Johnson and Brinkhurst 1971
		1968	1.32	0.264	
Conway	35.0	1967	0.67	0.235	
		1968	0.54	0.189	
Big Bay	5.0	1977	2.41[a]	0.121	C. K. Minns (unpubl. data)
Big Bay	6.0	1978	0.84[a]	0.050	
Glenora	20.2	1978	0.29[a]	0.059	
Limnocorral	4.0		2.9[a]	0.115	Charlton 1975

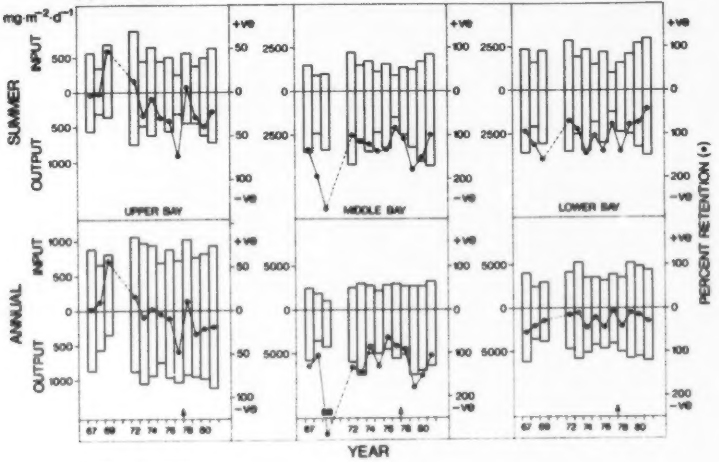
[a] Corrected for resuspension.
[b] Sinking rate = sedimentation rate × depth.

adjustments (Fig. 11a). The results for the upper Bay gave some indication of how closely the Cl budget can be balanced. Five of 13 annual budgets and 9 of 13 summer budgets were within 20%. The middle and lower Bay generally showed highly negative retentions, as expected. The levels tended to be fairly stable, indicating that the sectional exchange flows did not vary widely, as shown for the whole Bay (Table 7).

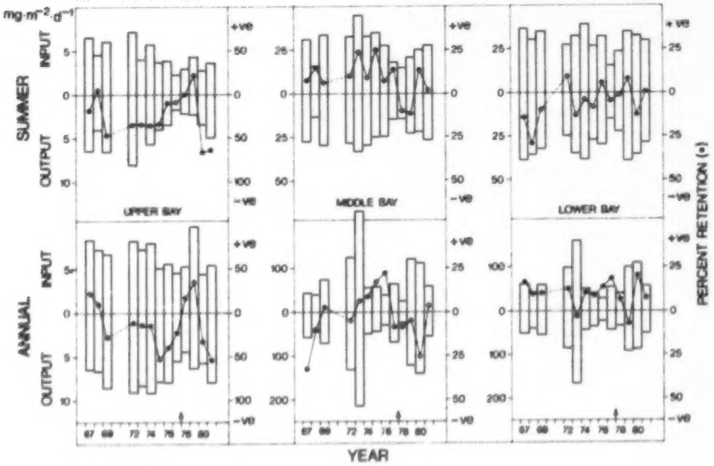
The reduction in point-source P loading was evident in the upper Bay summer budgets (Fig. 11b). Elsewhere with P, effects were not discernible. Retention rates were highly variable, but some characteristics were observed. Upper Bay P budgets tended to exhibit negative retentions, particularly in the summer, indicating that the sediments were a source of P. In the middle Bay, P retention was positive on average in the summer and the annual retention averaged near zero, and indicating that in the winter the sediments are a source of P removed by the high flushing regime. In contrast, lower Bay P retention averaged near zero in the summer, while indicating positive retention overall. In the lower Bay, summer retention was near zero because of the back flow-driven recirculation of P from the hypolimnion to the epilimnion.

With N retention (Fig. 11c), there appeared to be a shift from

(a) CHLORIDE



(b) PHOSPHORUS



(c) NITROGEN

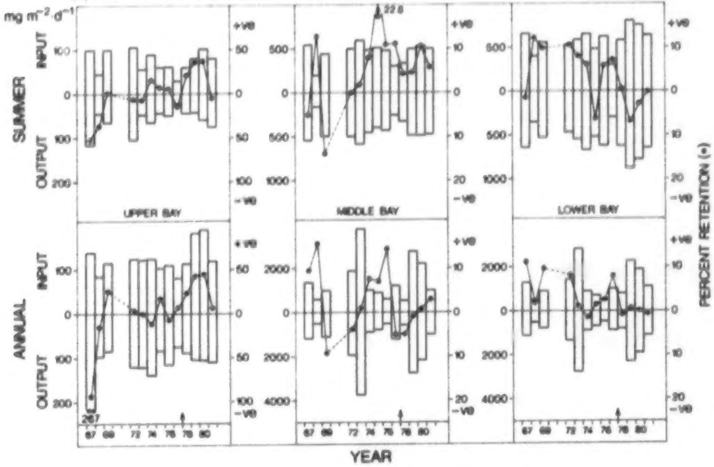


FIG. 11. Sectional annual and summer inputs, outputs, and retention values for 1967–69 and 1972–81 for (a) Cl (uncorrected), (b) P (corrected), and (c) N (corrected).

TABLE 9. Calculated summer mean sediment reflux rates (mg·m^{-2}·d^{-1}) for P and N in the three sections of the Bay.

	P			N		
Year	Upper	Middle	Lower	Upper	Middle	Lower
1967	9.7	9.3	5.3	160.1	134.9	137.7
1968	10.3	8.6	0.7	126.6	99.8	92.0
1969	10.8	11.0	14.1	178.7	20.5	84.1
1972	7.7	10.3	7.6	100.8	79.9	116.8
1973	11.3	17.0	1.1	122.0	87.0	82.8
1974	10.3	10.6	5.1	117.8	83.8	−24.9
1975	9.0	15.2	3.6	124.2	186.4	15.6
1976	8.0	8.0	6.8	107.8	117.2	24.3
1977	9.2	8.5	5.0	115.1	105.3	45.5
1978	6.0	4.3	3.9	90.4	76.2	−11.0
1979	8.1	2.8	1.7	124.6	95.6	−18.6
1980	5.7	8.0	−0.2	121.4	116.5	−1.2
1981	5.0	6.6	6.9	115.1	113.3	52.7

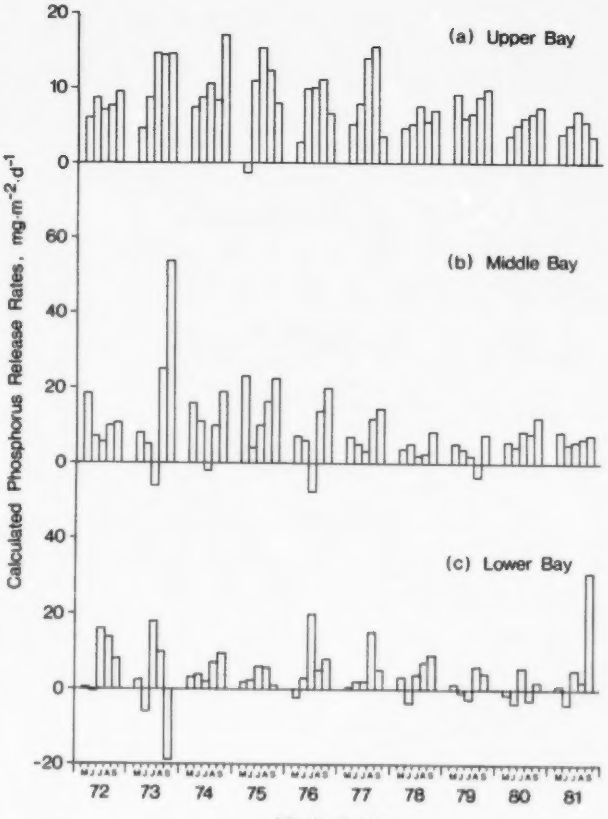


FIG. 12. Calculated P release rates, May to September, 1972–81, by Bay section.

zero to positive in the upper Bay after point-source P control, although the 1981 values dipped back toward the mean. In the middle and lower Bay sections, the range of retention values was much narrower (±10%) compared with the upper Bay (±50%). The middle Bay tended to have positive retention in the summer, while averaging zero on an annual basis. The lower Bay annual retention was often close to zero, while recently, summer retention tended to be more negative than earlier.

The calculated summer nutrient reflux rates (Table 9) showed the importance of sediment–water interaction. In the upper Bay the calculated sedimentation and reflux were greater (Fig. 12) than the external load and output (Fig. 11b). This reflux contributed to the net loss calculated for many years. In the middle and lower Bay the calculated reflux rates were generally less than input–output. On an annual basis these rates would have been of much less significance given the high annual flushing rates. Reflux rates were noticeably lower after P control (Fig. 12a, 12b). The middle and lower Bay reflux rates varied more widely, reflecting the uncertainties involved in the calculations. Overall, the range of calculated reflux rates spans the range encountered in oxygenated and anoxic situations elsewhere (Nurnberg 1984). Anoxia does not occur anywhere in BOQ (Minns and Johnson 1986) although the surface sediments are highly reduced (Damiani and Thomas 1974).

To reduce the effect of uncertainty in the analysis, we calculated composite annual and summer budgets for the pre- (1972–77) and post- (1978–81) control periods. The main uncertainties are winter (October to April), chemical concentrations in the Bay, and the magnitude of water exchanges between the Bay and Lake Ontario, given they were calculated on the basis of concentration differences. The 1967–69 data were excluded, as there were much fewer water quality data available. The budgets were assembled using the conceptual model (Fig. 10), and absolute values for each quantity were calculated (kilograms per day).

The composite budgets illustrate (Fig. 13) a number of features of and changes in the P and N budgets: (i) the P pool sizes thoughout the Bay have declined; (ii) the N pool size in the upper Bay has declined, but not elsewhere; (iii) sedimentation and reflux were generally of the same magnitude; (iv) Lake Ontario backflows dominated the input–ouput of nutrients in the middle and lower Bay; (v) prior to control, the upper Bay was a net exporter of P; since control, input has balanced output; (vi) the upper Bay shifted toward greater N retention after P control; and (vii) point-source P loading has decreased by 60–65%, while point-source N loading has decreased by about 10%.

Discussion

Loadings and Response

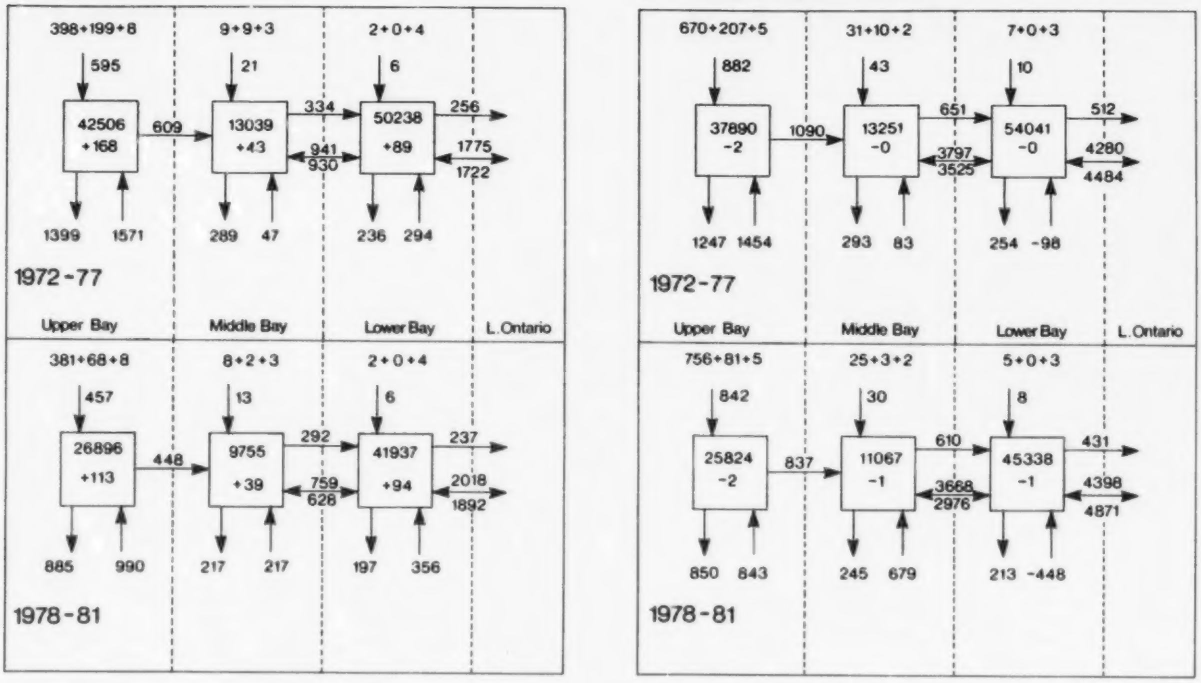
External P loading, whether to the upper or whole Bay, ranks among the highest in the Great Lakes and is high compared with some other locations (Table 10). In general, the bays of large lakes tended to be the focus for development in the past and thus received an unequal portion of increased P loading. Total annual loading has not declined appreciably in the Bay of Quinte since the introduction of P controls. However, when the influence of runoff is considered (Fig. 9), the percentage contribution of point-source inputs to total load has declined significantly, particularly in the critical summer period when runoff is low.

There can be no doubt that BOQ was and is eutrophic, but existing models such as the critical loading concept (Vollenweider 1976) are unable to cope with the conditions found there. Janus and Vollenweider (1981) pointed out that existing models relating loads and concentration of P cannot be used where hydraulic load is high and flushing regimes vary significantly seasonally. There can also be no doubt that the Bay has responded to reduced point-source loading: P concentrations are down (Robinson 1986), primary production has decreased, particularly in the upper Bay (Millard and Johnson 1986), and algal biomass is lower (Nicholls et al. 1986).

Considering the attributes by which the upper Bay differs from the rest of the Bay, e.g. shallowness and high flushing

(a) PHOSPHORUS – SUMMER

(b) PHOSPHORUS – ANNUAL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595
42506
+168
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21
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+43
334
941
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289
47
2+0+4
6
50238
+89
256
1775
1722
236
294
1972-77
Upper Bay
Middle Bay
Lower Bay
L. Ontario
381+68+8
457
26896
+113
448
885
990
8+2+3
13
9755
+39
292
759
628
217
217
2+0+4
6
41937
+94
237
2018
1892
197
356
1978-81
670+207+5
882
37890
-2
1090
1247
1454
31+10+2
43
13251
-0
651
3797
3525
293
83
7+0+3
10
54041
-0
512
4280
4484
254
-98
1972-77
Upper Bay
Middle Bay
Lower Bay
L. Ontario
756+81+5
842
25824
-2
837
850
843
25+3+2
30
11067
-1
610
3668
2976
245
679
5+0+3
8
45338
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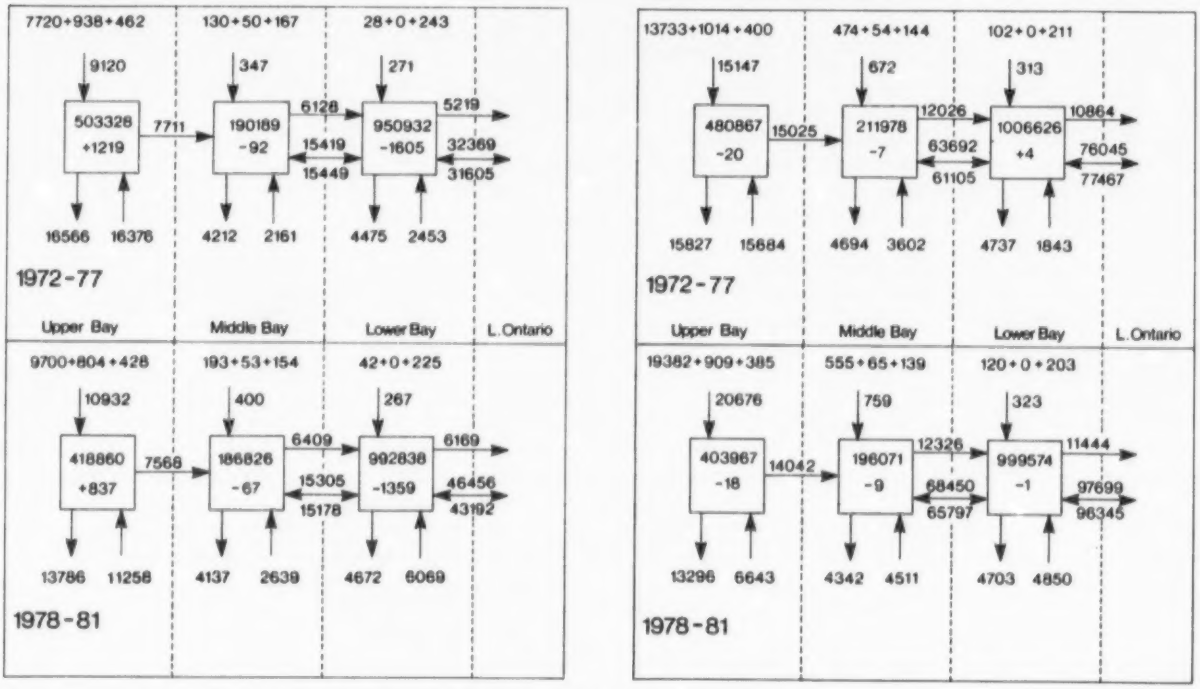
431
4398
4871
213
-448
1978-81

(c) NITROGEN – SUMMER

(d) NITROGEN – ANNUAL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+1219
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16566
16376
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190189
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15449
4212
2161
28+0+243
271
950932
-1605
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32369
31605
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1972-77
Upper Bay
Middle Bay
Lower Bay
L. Ontario
9700+804+428
10932
418860
+837
7568
13786
11258
193+53+154
400
186826
-67
6409
15305
15178
4137
2639
42+0+225
267
992838
-1359
6169
46456
43192
4672
6069
1978-81
13733+1014+400
15147
480867
-20
15025
15827
15684
474+54+144
672
211978
-7
12026
63692
61105
4694
3602
102+0+211
313
1006626
+4
10864
76045
77467
4737
1843
1972-77
Upper Bay
Middle Bay
Lower Bay
L. Ontario
19382+909+385
20676
403967
-18
14042
13296
6643
555+65+139
759
196071
-9
12326
68450
65797
4342
4511
120+0+203
323
999574
-1
11444
97699
96345
4703
4850
1978-81

FIG. 13. Average total pre- (1972–77) and post- (1978–81) control P and N budgets. The numbers are rates (kg·d^{-1}) and correspond by position to the budget components identified in Fig. 10.

TABLE 10. Comparative list of P loading data for various lakes and bays.

Location	Period	Annual P load $(\mathrm{g\,P\cdot m^{-2}\cdot yr^{-1}})$	Source
Bay of Quinte			
Upper	1972–77	2.37	This study
	1978–81	2.25	
Whole	1972–77	2.07	
	1978–81	2.35	
Lake Superior	1971–72	0.03	Vollenweider 1975
Lake Michigan	1971–72	0.10	
Lake Huron	1971–72	0.07	
Lake Erie	1971–72	1.10	
Lake Ontario	1971–72	0.86	
Lower Green Bay	Mid-1970's	1.26	Chapra and Sonzogni 1979
Saginaw Bay	Mid-1970's	1.04	
Western basin, Lake Erie	Mid-1970's	3.02	
Lake Washington	1964	2.33	Edmondson and Lehman 1981
	1976	0.49	
Lake Norviken	Precontrol	4.00	Ahlgren 1980
	Postcontrol	0.50	
Shagawa Lake	Precontrol	0.73	Malueg et al. 1975
Gravenhurst Bay	Precontrol	0.81–1.06	Dillon et al. 1978
	Postcontrol	0.31–0.46	

versus the exchange backflows of Lake Ontraio, it is appropriate to discuss the two parts separately before drawing some general conclusions.

Upper Bay

The lack of positive P retention (Fig. 13) in the upper Bay is the key to understanding P dynamics there. Phosphorus reflux from the sediment pool equals or exceeds the input from the water column via sedimentation. This, together with high flushing rates (Table 4), results in large quantities of P being exported. We contend that this situation has resulted from the interaction of two events, P enrichment of surface sediments over the last half century and the marked decline in the distribution and abundance of submerged macrophytes (SMs) in the late 1950's and early 1960's.

Our model is stated as follows. Increased point-source, external P loading gradually caused P enrichment of the surface sediments, which, in turn, caused an increase in P reflux, internal loading, particularly in the summer when reducing conditions prevail at the sediment–water interface. Ambient water P concentration ($[\mathrm{P}]_w$) increased due to rising external, and later internal, loading. Increased $[\mathrm{P}]_w$ promoted the buildup of algae, which, in turn, increased light extinction, which determines the depth distribution of SMs. Periods of low flushing exacerbate this situation. Low flushing was often associated with lower lake levels which further reduced the distribution of SMs, i.e. from the shoreline (currently, SMs occur in about 10% of the Bay area and the maximum possible extent has been estimated at about 20% (P. G. Sly and A. Crowder, pers. comm.)). The loss of SMs increased the effective wind fetch, allowing more sediment disturbance and freed sediment in the littoral zone which had formerly been sequestered along with its P. Then a greater movement of sediment led to increased export of sediment and P, and a greater mobility of resident sediment P. Thus, we arrive at the current state of affairs.

Once SMs have been lost, they have a slow recovery rate, and once sediments have been enriched with P, their replacement by dilution with new sediment associated with an external lower P load is a slow process (likely decades). Sediments do not become a net sink for P until new sediment reduces the pool of P available for reflux.

This model is an example of a cusp catastrophe (Fig. 14) (Woodcock and Davis 1978). This is a model where the response to one control factor is divergent depending on the level of a second control factor. At the extremes of the first factor, there are either smooth or abrupt shifts between states. Here, the first controlling factor is flushing rate, coupled with lake level, and the second is external P loading, coupled with internal loading. River nutrient loading is relatively unimportant because its associated flushing displaces equivalent amounts of nutrient (Johnson and Owen 1971). At low flushing rates, a hysteresis cycle is present, such that extreme loading changes are needed to switch between states. As loading increases, SM communities persist and sediment enrichment lags. Once a threshold for significant loss of macrophytes is exceeded, minor changes in loading, thereafter, will not significantly alter either the SMs or sediment P levels.

The support for this interpretation of events is a mixture of historical evidence from the Bay and analogy with evidence from elsewhere.

Prior to the 1950's, the upper Bay had an abundance of SMs. Abundance is thought (A. E. Christie, pers. comm.) to have increased in the late 1940's and early 1950's as P loadings began to accelerate. Hurley and Christie (1977) reported that as late as 1959, there were still luxuriant growths of SMs in areas of the Bay, such as the stretch from Trenton to Belleville. Soon after, during a period of low flow and low lake levels, SMs declined markedly and have remained so since (Crowder and Bristow 1986). Whillan (1979) attributed a similar marked decline of SMs in Burlington Bay, at the western end of Lake Ontario, occurring in 1962 and onwards, to lower lake levels, although increasing nutrient loads were also occurring.

The sequence of increasing and decreasing SMs associated with increasing eutrophication is similar to the order of events proposed by Wetzel and Hough (1973). Their sequence is one where overall primary production increases with increasing nutrient loadings, but the community of primary producers changes. First, there is a shift to greater contribution by SMs and associated epiphytic and eulittoral algae, and to a lesser extent by emergent macrophytes. At some point, the increase of

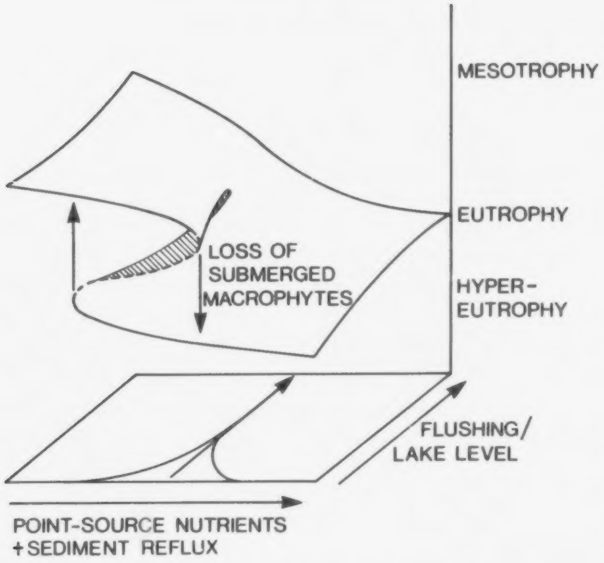

FIG. 14. Cusp catastrophe model of eutrophication in the upper Bay of Quinte where the control factors, nutrients, and flushing, interact to determine the trophic state.

SMs is cut off by algal-induced light extinction. Finally, SMs decline sharply and blue-green algae dominate. Wetzel and Hough (1973) considered that SMs were directly outcompeted by phytoplankton. Phillips et al. (1978) have proposed that SMs are stifled by the stimulated overgrowth of epiphytes and filamentous algae and that the "victory" of phytoplankton is coincidental.

SMs exert a stabilizing effect on their underlying sediments and reduce effective wind fetch in open water (Sculthorpe 1967). They also enhance sediment accumulation. After a decline in SMs, increased wind-induced mixing of sediments has two effects: SMs are inhibited from regaining a "foothold" and there is a greater likelihood that sediment will be exported, particularly in a shallow system such as the upper Bay. Damiani and Thomas (1974) found that the sediments in the mud accumulation zone of the upper Bay (34% of the bottom area) are short of fine-grained clay-size particles compared with sediments in Lake Ontario.

Prior to the loss of SMs, we would have expected to accumulate sediment and retain P. As eutrophication advanced (Minns 1986), the surface sediments became enriched with nutrients. Current levels are two to three times higher than original levels, based on core data (Warwick 1980; R. L. Thomas, pers. comm.). In the upper Bay, the sediments, apart from a thin oxygenated layer, are highly reduced (mean eH = 0.100 V) and rich in organic matter (Damiani and Thomas 1974). The resuspension reflux would be augmented in the summer by increased diffusive release of soluble P due to interface anoxia (Burns and Ross 1971) induced by increased inputs of organic matter due to primary production, higher temperatures, and periods of low wind stirring. Thus, as SMs decline, nutrient reflux, due to both resuspension and diffusion, peaks and matches or exceeds sedimentation. Our calculated reflux rates are similar to rates obtained by Lean and Charlton (1976) and Liao and Lean (1978a, 1978b) in controlled limnocorral experiments in BOQ, near Deseronto. The rates span the range recorded for oxygenated and anoxic systems (Nurnberg 1984).

The control of the P budget in the upper Bay has shifted from external to internal loading. While external P loading has been drastically reduced, internal P loading will decline slowly as sediment P is reduced. There is, of course, a link between external and internal loading.

If the state of the upper Bay is described by a cusp catastrophe, two recovery sequences can be considered. At low flushing rates, maximal reduction of point-source loading is needed to facilitate the recovery of macrophytes and reduction of sediment P. At high flushing rates, dilution effects improve water quality with even modest point-source reductions. Greater runoff reduces $[P]_w$ and is usually linked to greater sediment loads.

Flushing rates have been close to the average since 1978. Up to 1982, there was no evidence of any increase in macrophytes (Crowder and Bristow 1986), although in 1983 there were reports of increased growth in the middle Bay around Picton. It is not clear if the level of P control is sufficient to promote further recovery in the future through reductions in sediment P and increased macrophytes. Minns's (1986) model suggests that loading has been returned to an early 1950's level, when eutrophication was underway. Thus, while summertime algal biomass and $[P]_w$ have been reduced, the upper Bay may be locked into its current degraded state.

Middle and Lower Bay

The middle and lower sections of the Bay together form a freshwater estuary, and thus many of the generalizations concerning estuaries should apply. The two-layer flow with strong vertical mixing in the middle Bay and at the Glenora gap (Freeman and Prinsenberg 1986) resembles the features of a partially mixed estuary (Odum 1970; Dyer 1973). As with estuaries, upstream topographical constrictions, such as the Glenora gap, produce more mixing and greater velocities. Absence of mud and silt accumulation at the gap (R. L. Thomas, pers. comm.) is consistent with this. Typically, nutrients accumulate at depths lower down in an estuary, as sinking matter decomposes and then backflow and upstream upwelling returns the dissolved nutrients to the surface water for reuse in further production. Odum (1970, p. 357) described this phenomenon as a "nutrient trap", although "nutrient pump" may be a more appropriate term.

In the lower BOQ, dissolved nutrients, e.g. soluble reactive P, do accumulate at depth during the summer (Robinson 1986). Lake Ontario waters are typically low in dissolved P in the summer, so the source of accumulation lies within the Bay. Part is due to sediment reflux, but there must also be considerable decomposition of organic matter as it falls through the hypolimnion. Analysis of the oxygen depletion rates (Minns and Johnson 1986) in the lower Bay showed that the bulk of oxygen consumption took place in the water column.

Estuaries are noted for their high levels of production (Ketchum 1967; Odum 1970). BOQ is no exception. It has always been noted for its predominant contribution to the total fish harvest of Lake Ontario (Christie 1972). According to D. A. Hurley (pers. comm.), annual harvest in the Bay has generally been of the order of 10–20 $kg \cdot ha^{-1} \cdot yr^{-1}$, much above the 5 predicted by Ryder's (1965) morphoedaphic index, a widely accepted means of predicting sustainable yield in large temperate lakes. High levels of production have also been recorded for phytoplankton (Millard and Johnson 1986), zooplankton (Cooley et al. 1986), and benthos (Johnson and Brinkhurst 1971). Efficient recirculation of nutrients in a highly dynamic system is consistent with low net retention of nutrients.

In connection with the estuarine analogy, the role of flushing must be considered. Dillon (1975) demonstrated, in reference to lakes, that flushing must be incorporated along with the factors loading and depth used by Vollenweider (1975) when defining trophic status. In estuaries, flushing takes on an added importance, since the deep counterflows increase production. The adjusted budgets indicate that recirculation is several times greater than the upstream flow although it must be remembered that the upper Bay is the source of the "nutrient pump" nutrients. Lake Ontario is more dilute than the Bay, so that Bay – Lake Ontario exchanges cause a net loss of material. In fact, the Lake Ontario P concentrations have declined in the last few years (Internationasl Joint Commission 1978). The continuing combination of high flushing and nutrient regeneration engenders a stability of productivity which is apparent in the phytoplankton of the lower Bay. Algal biomass and production did not change as much in the lower Bay in response to P control (Millard and Johnson 1986).

Chapra (1979) has shown the importance of adjusting the usual nutrient-loading models for additional turbulent and advective exchanges when evaluating the trophic state of embayments. Specifically, he showed that in Saginaw Bay, an eutrophic bay on Lake Huron, the adjustment accounted for more than half the loading, similar to that observed in BOQ. In marine estuarine environments, the tides provide the energy for the mixing and exchanges. In large inland lakes, seiches and resonance provide this energy. Ahrnsbrak and Ragotzkie (1970) have described the effects of seiche-induced longitudinal mixing in Green Bay, Lake Michigan. They showed that the advective effect of the Fox River inflow, the main input, was insignificant in summer, but dominated in the winter. Similar phenomena have been demonstrated at Chequamegon Bay, Lake Superior, and South Bay, Lake Huron. Thus, the "nutrient pump" recirculation of nutrients, comparable with sediment release in the upper Bay, is probably the most important component of the lower Bay's P budget.

The physical processes operating in the lower Bay have significance in assessing the recovery pattern of the Bay as a whole. The counterflow and nutrient recycling make the lower Bay equally dependent on the upper Bay output and Lake Ontario exchanges, indicating that there should be a smaller response to reductions in external loadings upstream. This prognosis would also indicate that the oxygen depletion rates will respond slowly, if at all, to enhanced P removal at the point sources, since they should, to a large degree, reflect the "nutrient pump" phenomenon (Minns and Johnson 1986).

Conclusion

Warwick's (1980) paleolimnological analysis of a core taken below Glenora suggests that the lower Bay followed a course from oligotrophy in the late eighteenth century through to the mesoeutrophy of today. The upper Bay likely followed a similar course, but "broke through" (Fig. 14) to a hypereutrophic state. Minns's (1986) historical reconstruction illustrated the timing of this event. The combination of rapid urban growth and increased detergent use after 1945 led to the conditions of the early 1960's. This present study illustrates the importance of external and internal loading, and recirculation of nutrients. While significant improvements in water quality have resulted from the controls on point-source inputs of P, there is every reason to expect further improvements as the internal reflux shifts to a new steady state with external loading. Many of the worst eutrophication problems of the Great Lakes and elsewhere occur in bays and estuaries, such as BOQ, and these are the places where our success in understanding and overcoming these problems must be greatest.

References

Ahlgren, I. 1980. A dilution model applied to a system of shallow eutrophic lakes after diversion of sewage effluents. Arch. Hydrobiol. 89: 17–32.

Ahrnsbrak, W. F., and R. A. Ragotzkie. 1970. Mixing processes in Green Bay. Proc. 13th Conf. Great Lakes Res. 1970: 860–890.

Burns, N. M., and C. Ross. 1971. Nutrient relationships in a stratified eutrophic lake. Proc. 14th Conf. Great Lakes Res. 1971: 749–760.

Chapra, S. C. 1979. Applying phosphorus loading models to embayments. Limnol. Oceanogr. 24(1): 168–171.

1982. A budget model accounting for the positional availability of phosphorus in lakes. Water Res. 16: 205–209.

Chapra, S. C., and W. C. Sonzogni. 1979. Great Lakes total phosphorus budget for the mid 1970's. J. Water Pollut. Control Fed. 51: 2524–2533.

Charlton, M. N. 1975. Sedimentation: measurements in experimental enclosures. Verh. Int. Ver. Limnol. 19: 267–272.

Christie, A. E. 1973a. Phytoplankton studies in the Bay of Quinte I. Physical chemical and phytoplankton characteristics. Ont. Minist. Environ. Res. Rep. No. W44: 55 p.

1973b. Phytoplankton studies in the Bay of Quinte II. Relationships between seston-phosphorus, nitrogen, carbon and phytoplankton. Ont. Minist. Environ. Res. Rep. No. W45: 30 p.

Christie, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

Cooley, J. M., J. E. Moore, and W. T. Geiling. 1986. Population dynamics, biomass, and production of the macrozooplankton in the Bay of Quinte during changes in phosphorus loadings, p. 166–176. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Crowder, A., and M. Bristow. 1986. Aquatic macrophytes in the Bay of Quinte, 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Damiani, V., and R. L. Thomas. 1974. The surficial sediments of the Big Bay section of the Bay of Quinte, Lake Ontario. Can. J. Earth Sci. 11: 1562–1576.

Dillon, P. J. 1974. A critical review of Vollenweider's nutrient budget model and other related models. Water Res. Bull. 10(5): 969–989.

1975. The phosphorus budget of Cameron Lake, Ontario: The importance of flushing rate to the degree of eutrophy of lakes. Limnol. Oceanogr. 20(1): 28–39.

Dillon, P. J., K. H. Nicholls, and G. W. Robinson. 1978. Phosphorus removal at Gravenhurst Bay, Ontario: an 8-year study on water quality changes. Verh. Int. Ver. Limnol. 20: 263–271.

Dyer, K. R. 1973. Estuaries: a physical introduction. Wiley, London. 140 p.

Edmondson, W. T., and J. J. Lehman. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnol. Oceanogr. 26: 1–29.

Freeman, N. G., and S. J. Prinsenberg. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Hurley, D. A., and W. J. Christie. 1977. Depreciation on the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

International Joint Commission. 1978. Great Lakes Water Quality Board Annual Report. International Joint Commission, Windsor, Ont.

Janus, L. L., and R. A. Vollenweider. 1981. Summary Report: The OECD Co-operative Programme on Eutrophication (Canadian Contribution). DOE IWD Sci. Ser. No. 131.

Johnson, M. G., and R. O. Brinkhurst. 1971. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1699–1714.

Johnson, M. G., and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43(5): 836–853.

Ketchum, B. H. 1967. Phytoplankton nutrients in estuaries, p. 329–335. *In* G. H. Lauf [ed.] Estuaries. AAAS, Washington, DC.

Kuntz, K. W. 1980. Atmospheric bulk precipitation in the Great Lakes Basin. DOE IWD Sci. Ser. No. 115: 27 p.

Lean, D. R. S., and M. N. Charlton. 1976. A study of phosphorus kinetics in a lake ecosystem, p. 283–294. *In* J. O. Nriagu [ed.] Environmental biogeochemistry. Vol. I. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

Liao, C. F.-H., and D. R. S. Lean. 1978a. Nitrogen transformations with the trophogenic zone of Lakes. J. Fish. Res. Board Can. 35: 1102–1108.

1978b. Seasonal changes in nitrogen compartments of lakes under different loading conditions. J. Fish. Res. Board Can. 35: 1095–1101.

Malueg, J. W., D. P. Larsen, D. W. Schultz, and T. T. Mercier. 1975. A six-year water, phosphorus and nitrogen budget for Shagawa Lake, Minnesota. J. Environ. Qual. 4(2): 236–242.

McCombie, A. M. 1967. A recent study of the phytoplankton of the Bay of Quinte, 1963–64. Proc. 10th Conf. Great Lakes Res. 1967: 37–62.

Meredith, D. D. 1975. Predictive models for Great Lakes hydrology. Water Res. Bull. 11(3): 526–535.

Millard, E. S., and M. G. Johnson. 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K. 1986. Total phosphorus loading to the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., and M. G. Johnson. 1979. Temporal variation in the nutrient export of rivers draining into the Bay of Quinte, Ontario, Canada. Water Res. Bull. 15(4): 1061–1072.

1986. Temperature and oxygen conditions and oxygen depletion in the Bay of Quinte, Lake Ontario, p. 40–49. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nurnberg, G. K. 1984. The prediction of internal phosphorous load in lakes with anoxic hypolimnia. Limnol. Oceanogr. 29(1): 111–129.

Odum, W. E. 1970. Insidious alteration of the estuarine environment. Trans. Amer. Fish. Soc. 99(4): 836–847.

Ontario Ministry of the Environment. 1975. Outlines of analytical methods. Ontario Ministry of the Environment, Toronto, Ont.

Phillips, G. L., D. F. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. Aquat. Bot. 4: 103–126.

Prinsenberg, S. J. 1978. Free oscillations in the lower Bay of Quinte. Fish. Environ. Can. Res. Dev. MS. Rep. Ser. No. 7: 93 p.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Ryder, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. Arnold, London. 610 p.

Shiomi, M. T., and K. W. Kuntz. 1973. Great Lakes precipitation chemistry: Part I, Lake Ontario basin. Proc. 16th Conf. Great Lakes Res. 1973: 581–602.

Vollenweider, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to phosphorus and nitrogen as factors in eutrophication. OECD Tech. Rep. DAS/CSI/68.27: 159 p.

1975. Input–output models (with special reference to the phosphorus loading concept in limnology). Schweiz. Z. Hydrol. 37: 53–84.

1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53–83.

Warwick, W. F. 1980. Paleolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 117 p.

Wetzel, R. G., and R. A. Hough. 1973. Productivity and role of aquatic macrophytes in lakes. An assessment. Pol. Arch. Hydrobiol. 20: 9–19.

Whillan, T. H. 1979. Historic transformations of fish communities in three Great Lakes bays. J. Great Lakes Res. 5(2): 195–215.

Woodcock, A., and M. Davis. 1978. Catastrophe theory. Avon Books, New York, NY. 151 p.

Total Phosphorus Loading to the Bay of Quinte Between the Years 1800 and 2000: A Model Study

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Minns, C. K. 1986. Total phosphorus loading to the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

The models generally used, such as Vollenweider's, to evaluate phosphorus eutrophication in lakes and bays cannot be used on the Bay of Quinte because of its extreme morphometry and hydrology. Another, simple model is developed which uses population growth in urban centres and in the watershed to predict changes in river and point-source loadings of phosphorus. The role of the variable runoff is examined. Predicted annual loads and mean summer input concentrations are consistent with available data. The model demonstrates the importance of controlling point sources and shows how loading escalated after the 1940's because of increasing urban populations and the use of phosphate detergents. The model also shows how the control measures, first the reduction of P in detergents and then installation of testing treatment, greatly reduced point-source inputs. The model shows how low summer flows and high point-source inputs produce excessive P concentrations in the summer and demonstrates the importance of consistent control for the preservation of water quality. If all P removal facilities are operated efficiently, it is predicted that summer P concentrations in the Bay of Quinte will be kept below 50 $\mu g \cdot L^{-1}$ well into the next century, under most flow conditions.

Les modèles qu'on utilise généralement pour évaluer le phénomène d'eutrophisation par le phosphore dans les lacs et les baies (tels que celui de Vollenweider) ne peuvent être employés dans la baie de Quinte en raison du caractère morphométrique et hydrologique très prononcé de celle-ci. On élabore un autre modèle simple, qui fait appel à l'accroissement de la population dans les centres urbains et dans le bassin versant pour prédire les changements dans la rivière et dans les charges ponctuelles de phosphore. On examine le rôle de la variabilité du ruissellement. Les charges annuelles prévues et les apports moyens pendant l'été concordent avec les données disponibles. Le modèle montre l'importance de réduire les sources ponctuelles et la façon dont les charges ont augmenté après les années 40 en raison de l'accroissement des populations urbaines et de l'utilisation de détersifs à base de phosphate. Le modèle montre également de quelle façon les mesures de réduction, d'abord la diminution de la quantité de P dans les détersifs, puis l'installation d'un dispositif de traitement expérimental, ont permis de réduire considérablement les apports ponctuels. Il montre aussi de quelle façon les faibles débits d'été et les apports ponctuels importants entraînent des concentrations excessives de P en été et démontre l'importance d'un contrôle constant pour préserver la qualité de l'eau. Si l'on exploite efficacement tous les dispositifs utilisés pour l'enlèvement du P, on prévoit que les concentrations de P pendant l'été dans la baie de Quinte demeureront inférieures à 50 $\mu g ; L^{-1}$ pendant une bonne partie du prochain siècle, pour ce qui est de la plupart des régimes d'écoulement.

Introduction

In freshwater systems where eutrophication has occurred, and has perhaps been controlled, measurements of nutrient loading and concentration are usually available only for the current period when the problem receives attention. Selecting an appropriate level of nutrient control for a particular water body is difficult when data for the times before the problem developed are lacking. The practice has been to rely on empirical criteria such as those described by Vollenweider (1968), which are based on comparisons among a large number of water bodies. However, this approach has limitations, especially when dealing with hydrological and morphometric extremes. Janus and Vollenweider (1981), in examining the results of the OECD Co-operative Programme on Eutrophication, identified system characteristics which preclude the use of diagnostic methods developed to assess eutrophication in the OECD study. These characteristics include high flushing rates ($> 2 \cdot yr^{-1}$), irregular seasonal or secular flushing regimes, high turbidity, and significant internal nutrient loading where dynamic equilibrium with respect to nutrient loadings has not been reached. Detailed analysis of nutrient budgets in the Bay of Quinte indicates that all the above conditions are present (Minns et al. 1986).

Another approach to setting nutrient control targets is to develop historical estimates of the loadings and concentrations, which can then be matched to reported trends of water quality deterioration. Chapra (1977, 1980) presented such an approach for the Great Lakes where population growth and land-use changes were used to estimate loadings.

A similar modelling approach has been used in this study which predicts changes in total phosphorus loadings and input concentrations for the Bay of Quinte, from the period of human settlement, ca. 1800, through the present period and on to 2000. Loads and concentrations expected in the future are compared with values estimated for the past, and the expected degree of restoration assessed. The importance of secular and seasonal variation in runoff is examined.

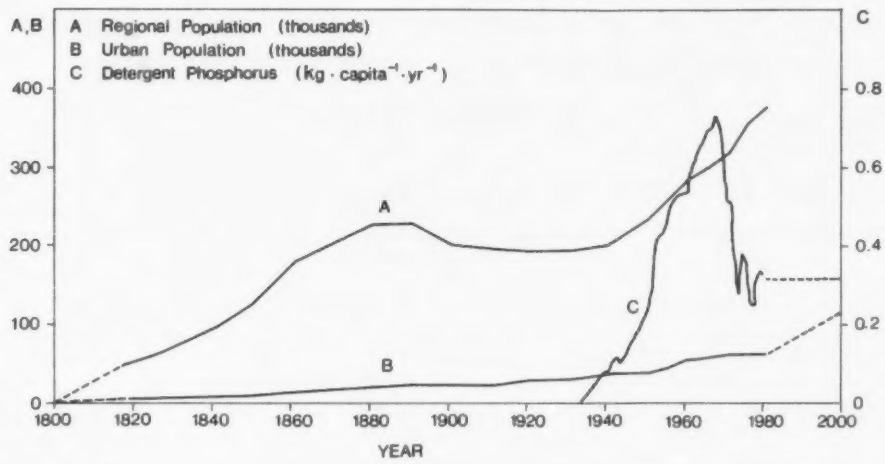

FIG. 1. Trends in regional and urban population and detergent P use, 1800–2000.

TABLE 1. River drainage information for the Bay of Quinte watershed.

			Land use				River [P]	(mg · m^{-3})
River	Drainage (km^2)	Period of gauging	Urban (%)	Agriculture (%)	Forest (%)	Sedimentary (%)	Present[a]	Original[b]
Trent	12 549	1950 on	1.0	36.1	59.7	53	41.3	17.2
Moira	2 737	1916 on	0.6	26.6	69.4	30	32.6	14.0
Salmon	898	1959 on	0.4	31.9	62.7	45	25.2	16.1
Napanee	787	1916–25, 1947 on	1.1	40.5	56.2	39	40.0	15.2
Wilton	127	1966 on	0.3	74.5	23.3	100	63.2	23.7
Total	18 182		1.0	37.1	58.7			

[a] Geometric mean of measured values, 1965–81, above the urban centres.

[b] Derivation is described in the text.

Loadings and Concentration Model

Phosphorus inputs to the Bay were assumed to come from two sources, rivers and urban centres on the Bay. Atmospheric loading was ignored, since direct loading represents less than 2% of recent total loading (Minns et al. 1986). Obviously when river loadings were lower, the proportion could have been higher. However, at the Bay of Quinte river sources tend to overwhelm others and likely atmospheric loading was lower in earlier times.

Point-source inputs were calculated on the basis of domestic P waste (C_H, milligrams P per day) and the use of P containing cleaning compounds, mostly detergents ($C_D(t)$, milligrams P per day). This was multiplied by the urban population ($N(t)$) and by $(1 - R(t))$, where R is the P removal efficiency at sewage treatment plants. Human P waste was set at $0.55\ \mathrm{kg \cdot capita^{-1} \cdot yr^{-1}}$ ($1.51\ \mathrm{mg \cdot d^{-1}}$) (Dillon and Rigler 1975). This value was taken by Dillon and Rigler to represent per capita output given secondary treatment in a sewage treatment plant without P removal. The use of detergents was estimated for the period 1935–80 (Fig. 1) based on material and production data complied by Statistics Canada (Publ. No. 46–214). Urban inputs come from Trenton, Belleville, Deseronto, Napanee, and Picton.

Census populations up to 1981 come from the records of the Legislature of Upper Canada and Statistics Canada (Fig. 1). Urban growth from 1981 to 2000 was derived from projections of most probable populations produced by the Ontario Ministry of Treasury, Economics and Intergovernmental Affairs. The main population growth in the future is expected to occur in Belleville and Trenton.

Phosphorus removal efficiency (R) at sewage treatment plants was assumed to be zero from 1800 until 1977 and, initially, it was projected to be 0.7 (equivalent to a final effluent with 1 mg $\mathrm{P \cdot L^{-1}}$) from 1978 onwards. In all years, all point-source P was assumed to be potential loading.

Estimating P removal efficiency over such a long time span is difficult. In the nineteenth century there were no sewer systems, so a large part of point-source P was not discharged into the Bay; thus, the per capita P output, although adjusted to assume secondary treatment, probably overestimated this input. Belleville, the largest source, installed sewers at the beginning of the twentieth century, but probably not all of the population was served. Later, P discharges were reduced as some sewage treatment was implemented but at the same time were increased as more of the growing population was connected to the sewer system. The assumptions in the model are a compromise, and probably most accurate after 1940 when inputs increased sharply.

Five gauged rivers flowing into the Bay account for 94% of the total drainage (Table 1). The smallest, Wilton Creek, was assumed to be representative of the several small drainage areas

TABLE 2. Estimated[a] low, mean, and high annual and summer flows ($m^3 \cdot s^{-1}$).

River	Annual			Summer		
	Low	Mean	High	Low	Mean	High
Trent	81.5	132.6	215.5	28.5	61.0	130.7
Moira	17.5	30.0	51.4	2.5	8.3	27.7
Salmon	5.9	10.4	18.3	0.5	2.4	11.2
Napanee	5.2	9.0	15.7	0.7	2.3	7.4
Wilton	0.8	1.4	2.4	0.1	0.2	0.8
Total	117.4	194.9	323.9	32.7	76.1	184.8

[a] Low ($\hat{\mu} - 2\hat{\sigma}$), mean ($\hat{\mu}$), high ($\hat{\mu} + 2\hat{\sigma}$) from log-transformed data, 1916–81.

which make up the remaining 6%. Inflow for any period was calculated by summing the flows of the four large rivers and 9.51 (ratio of Wilton and miscellaneous to Wilton drainage areas) times the Wilton Creek flow. Since the Moira River had been gauged the longest (since 1916), month by month $\log_e/\log_e$ regressions of mean monthly flows were used to estimate mean monthly flow of the other rivers from 1916 to 1981, where gaps existed. Logarithmic means and standard deviations were then used to estimate likely low, mean, and high annual runoff (Qa) and summer (June to September) runoff (Qs) (Table 2). Low and high flows were calculated from the mean ± two standard deviations. Therefore in the model, the low, mean, and high flows were used for the period 1800–2000. In addition, the measured or estimated flows were used year by year, from 1916 to 1981.

The land-use changes which affected river [P], and regional population growth, were assumed to have occurred synchronously in the drainage basin. Presettlement [P] values were used for 1800, and present-day values were used for 1971 onwards. From 1801 to 1970, [P] values were changed between these two limits directly in proportion to the regional population (Fig. 1) of the counties which made up the bulk of the drainage area (Northumberland, Peterborough, Hastings, Lennox and Addington, Victoria, and Prince Edward).

Presettlement [P] values were estimated using average values reported by Dillon (1974) and Dillon and Kirchner (1974) for unpopulated forested, igneous and sedimentary, watersheds which lie in the western part of the Trent River drainage. The average [P] values used were 9.8 and 23.7 $\mu g \cdot L^{-1}$ for igneous and sedimentary basins, respectively, and the value for each river draining into the Bay was calculated according to the proportion of each rock type in its drainage (Table 1). Present-day values used were the log-mean of values recorded above the urban centres by the Ontario Ministry of the Environment, 1965–81 (Table 1), and so were unaffected by urban runoff of sewage.

The model equations are as follows:

$$(1)\quad La = \left[\sum_{1}^{5} Pi(t)\,Qai(t) + N(t)\cdot(C_H + C_D(t)) \times (1 - R(t))\right] \Big/ A$$

$$(2)\quad Ps = \left[\sum_{1}^{5} Pi(t)\,Qsi(t) + N(t)\cdot(C_H + C_D(t)) \times (1 - R(t))\right] \Big/ \Sigma Qsi(t)$$

where La = annual P loading (milligrams per square metre per day), Ps = mean summer input [P] (micrograms per litre), Qai = annual flow (cubic metres per day) for river i, Qsi = summer flow (cubic metres per day) for river i, $Pi(t)$ = [P] for river i in year t, $N(t)$ = urban population in year t, C_H = human P output (milligrams per day), $C_D(t)$ = detergent use (milligrams per day) in year t, $R(t)$ = P removal efficiency in year t, and A = surface area of the Bay (square metres).

Results

The model predicted that annual P loading has increased markedly since 1800 (Fig. 2). The initial rise coincided with the deforestation of the drainage basin and the subsequent expansion of agriculture. Population growth faltered after 1880 (Fig. 1) with the decline of the lumber industry and only resumed after the Depression of the 1930's. Regional population rose most sharply in the period 1940 to present with the main urban growth coming in the 1950's. The rise in urban population coincided with a rapid increase in the use of P-based detergents (Fig. 1). Peak use came in 1968, with 0.73 kg $P \cdot capita^{-1}$, after a linear increase from 1935. Phosphate use declined after the enactment of regulation and controls in 1971.

In the model, the mean annual P loading went from 0.67 $mg \cdot m^{-2} \cdot d^{-1}$ in 1800, through 2.36 in 1890, to a peak of 3.42 in 1969. After detergent P reductions were in place, per capita use ranged from 0.25 to 0.38 $kg \cdot yr^{-1}$ with a mean of 0.32 which was assumed to apply for the period 1981–2000. Model P loading drops to a mean of 3.17 $mg \cdot m^{-2} \cdot d^{-1}$ in 1977, and with the implementation of 0.7 removal in 1978, loading drops to 2.81. The model then predicts loading would rise again to 2.96 in the year 2000.

Predicted loadings were similar to measured loadings for the period 1965–81 (Fig. 3), presented by Minns et al. (1986). Changes to land use have brought about the greatest absolute loading changes, from 1.1 $mg \cdot m^{-2} \cdot d^{-1}$ in 1800 to 2.65 in the 1970's. Point-source input peaked at 0.81 $mg \cdot m^{-2} \cdot d^{-1}$ in 1968–69, declined to 0.52 in 1977, and dropped to 0.16 in 1978 with the implementation of 0.7 removal.

Vollenweider (1976) defined critical P loading as follows:

$$LC(mg \cdot m^{-2} \cdot d^{-1}) = 10 \text{ to } 20 \cdot \left(\frac{Qa}{A}(1 + \sqrt{V/Qa})\right)$$

where Qa = runoff (cubic metres per day), A = area (square metres), and V = volume (cubic metres). For the Bay of Quinte, Vollenweider's model predicts a critical loading range of 1.1–2.2 mg $P \cdot m^{-2} \cdot d^{-1}$, using mean annual runoff. However, the model predicted a mean load of 1.1 in 1800 and passed the 2.2 level by 1880. According to paleoecological results (Warwick 1980; Stoermer et al. 1985) the Bay became eutrophic in the 1850–1900 period. However, the more obvious effects of eutrophication (loss of fish and macrophytes) did not occur until after 1940. This illustrates the limitations of general

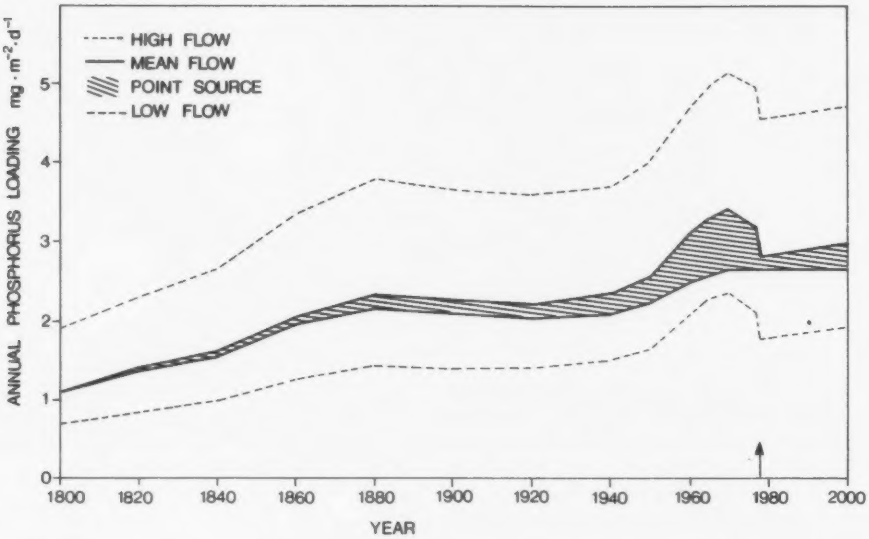

FIG. 2. Projected annual P loading to the Bay of Quinte, 1800–2000. The arrow marks the start of P removal.

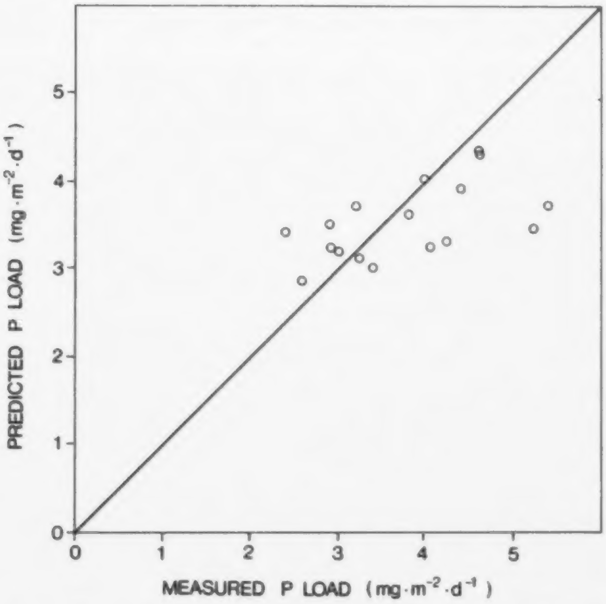

FIG. 3. Comparison of predicted and measured P loadings to the Bay of Quinte, 1965–81.

eutrophication models as pointed out by Janus and Vollenweider (1981).

Johnson and Owen (1971) pointed out the significance of net nutrient loading, in their analysis of the 1968 P budget for the Bay of Quinte. In the Bay, river inputs of P are largely displayed by flushing due to the accompanying runoff. Point-source loading is highly concentrated and serves primarily to raise ambient concentrations. Runoff to the Bay is generally low in the summer, when most biological activity occurs and thus when most problems due to eutrophication occur. Consequently, it is point-source loading which has the greatest impact upon the Bay's water quality.

The model predicted that the mean summer input concentration (*Ps*) rose steadily from 17 $\mu g \cdot L^{-1}$ in 1800 to between 37 and 42 in the period 1880–1940 (Fig. 4). After 1940, *Ps* rose to a peak of 72 in 1969, declined to 61 in 1977, and dropped to 47 in 1978. By 2000, the model predicted a rise back to 53 $\mu g \cdot L^{-1}$ (line A, Fig. 4), assuming 70% removal efficiency was roughly equivalent to producing a final sewage effluent with 1 mg $P \cdot L^{-1}$. In historical terms, the 1978 value was equivalent to returning to the 1950 state, and the 2000 value took the Bay back to the 1955 point.

The model's year by year predictions of mean summer input concentration (*Ps*) also compare favourably with mean summer [P] values recorded in the Bay at Belleville in the upper Bay (Fig. 5) for the period 1972–81. If P retention were occurring, in-Bay concentrations would be expected to be less than input concentrations. In the upper Bay of Quinte there was little retention in the 1972–81 period (Minns et al. 1986).

Alternative future scenarios were then examined given the possibilities that (1) detergent P use would drop to 0.25 kg $P \cdot capita^{-1} \cdot yr^{-1}$ and/or (2) a 90% P removal efficiency, equivalent to 0.5 mg $P \cdot L^{-1}$ in final effluent. The latter is an option that is already in use at some treatment plants on the Bay during the summer months. The model predicts that further control of phosphate detergent use would have relatively little impact on *Ps* (Table 3). The effects of detergent phosphate restrictions will likely be offset by the rising use of automatic dishwashers, which generally rely on P-based cleaning agents. In contrast, the model predicts that improving the removal efficiency at the sewage treatment plants would reduce the *Ps* in 2000 to the 1946 level (Table 3). A gradual shift from 70 to 90% removal between 1978 and 2000 would tend to produce a further decline in *Ps* (line B, Fig. 4).

Model estimates of annual loading and *Ps* under low and high flow regimes (Fig. 2 and 4) illustrate the importance of runoff variability. In the case of *Ps*, as point-source contributions increased, the range of potential *Ps* increased markedly. Further, the year by year estimates from 1916 to 1981 show that sustained departures from the mean flow could exacerbate effects. While both annual and summer runoff are highly variable, there

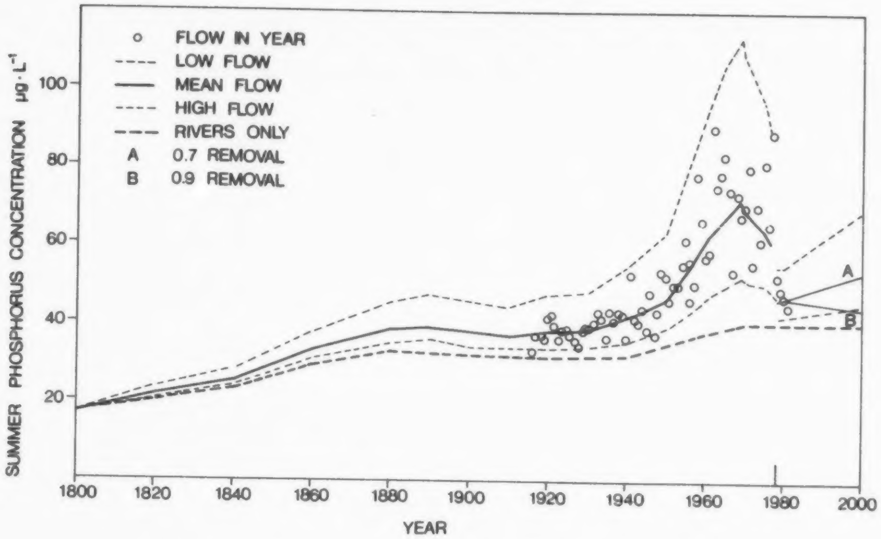

FIG. 4. Predicted summer inflow [P], *Ps*, at Belleville, 1800–2000.

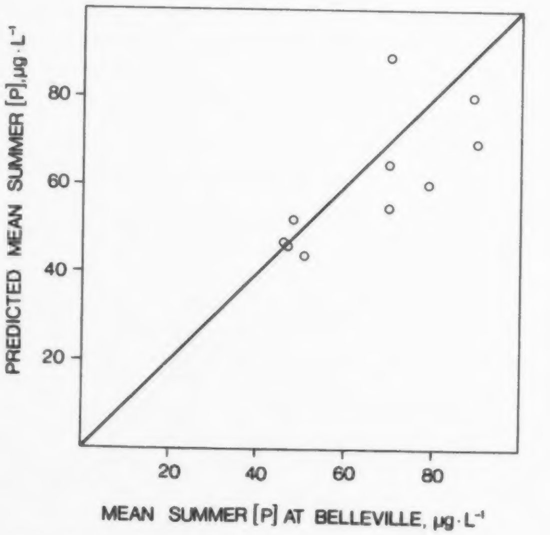

FIG. 5. Predicted mean summer input P concentration (*Ps*) versus mean summer [P] at Belleville in the upper Bay, 1972–81.

tend to be runs of low summer flows such as occurred in the early 1960's (Fig. 6).

Discussion

These results put recent efforts to control P in the Bay of Quinte into a broader context. Evidence of advancing eutrophication was available from the late 1940's onward. Tucker (1948) showed the presence of a eutrophic algal community in the lower Bay along with measurable oxygen depletion in the hypolimnion. Johnson and Owen (1971) have described the conditions which existed in 1968 when recommendations were made for construction of new sewage treatment facilities. Hurley and Christie (1977) stated that in the 1950's, fishermen began to complain of algal slimes on gill nets, and Christie (1972) has loosely attributed the demise of the large walleye fishery to direct and/or indirect effects of eutrophication in the 1950's. In addition, there is a general observation of the rise and fall of submergent macrophytes during the 1950's (W. J. Christie, Glenora Fisheries Station, pers. comm.). From the 1930's onward, the Belleville filtration plant had to use strainers to clean the water supply prior to treatment (D. A. Hurley, Glenora Fisheries Station, pers. comm.). These events are correlated with the growth of urban populations, installation of sewer systems, and the rise in the use of phosphate detergents.

An earlier rise in the loading occurred as the land was cleared for agriculture, changing the Bay from meso-oligotrophic to eutrophic, as shown by Warwick (1980) in his detailed analysis of the chemical and biological chronology in a sediment core taken at Glenora in the lower Bay. The decline of the salmonids and then the coregonids in the nineteenth century lead to the development of a warm-water percid/esocid fishery. The Bay ecosystem was able to withstand that change in the period 1800–1930, and yet still provide acceptable water quality and fisheries. However, the recent shift to hypereutrophy in the upper Bay degraded the water quality and fisheries beyond acceptable limits.

The introduction of detergent P limitations and the installation of tertiary treatment plants have prevented the worst excesses of hypereutrophication. However, future population growth will bring about a return of the 1950–55 conditions if additional measures for P control are not implemented. The alternative scenarios indicated that enhanced tertiary P removal equivalent to 90% (or 0.5 mg $\cdot$ L^{-1} final effluent concentration) would significantly improve the situation. This has been the summertime objective since 1978. Studies by Johnson et al. (1978) on the relationship between land use activities and P loading have indicated that municipal point-source removal of total P down to 0.5 mg $\cdot$ L^{-1} final effluent is the most cost-effective control measure for further reducing P loading once the 1.0 mg $\cdot$ L^{-1} objective has been met.

To maintain satisfactory water quality, loading rates must be held constant, after allowing for runoff variation. This is difficult to achieve if the population continues to grow, since P

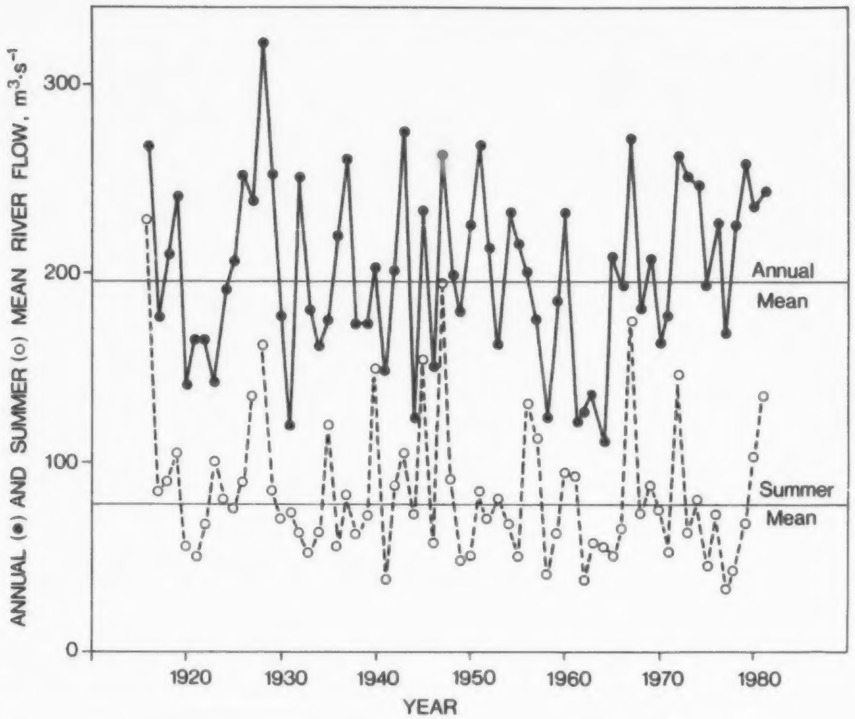

FIG. 6. Estimated annual and summer runoff into the Bay of Quinte, 1916–81.

TABLE 3. Predicted mean summer input P concentrations (Ps, $\mu g \cdot L^{-1}$) in the year 2000 under different P control scenarios and a range of flow regimes.

Control scenario		Flow regime[a]			
P removal efficiency (%)	Detergent P use ($kg \cdot capita^{-1} \cdot yr^{-1}$)	Low	Mean	High	Equivalent precontrol year
70	0.321	69.3	52.7	45.0	1955
70	0.250	67.0	51.7	44.6	1953
90	0.321	50.2	44.5	41.6	1946
90	0.250	49.5	44.2	41.5	1946

[a] See Table 2.

removal facilities are designed to produce effluents with a P concentration below an assigned target, but not designed to limit the volume of that effluent. On the Bay of Quinte, new tertiary treatment facilities have significantly reduced the current point-source loading, but that load will gradually increase with the increase in population. As indicated above, reduction of the final effluent concentration from 1 to 0.5 $mg \cdot L^{-1}$ can contain the situation through to the year 2000. Beyond that, additional control measures will be needed. Studies reported by Johnson et al. (1978) and IJC (1978) indicate that further control of point-source effluents is expensive and that the other significant sources of P, such as diffuse agricultural releases, must be controlled. In the Lake Ontario drainage, a large part of which is the Bay of Quinte drainage, agriculture is estimated to account for 66% of the diffuse river inputs (IJC 1978). In the lower Bay drainage, the land is farmed intensively and includes many dairy farms. The IJC report indicates that significant P loading reductions could be achieved through improved farming practices and soil conservation measures. Overall, however, the largest reductions can currently be achieved through effective point-source controls.

The most drastic changes in the Bay of Quinte ecosystem are the decline of large piscivores, particularly the walleye (*Stizostedion vitreum vitreum*), the increasing algal biomass, and the rise and fall of submergent macrophytes. All these changes occurred in the 1950's, as the mean summer input [P] exceeded 50 $\mu g \cdot L^{-1}$. This value has been indentified before as a critical level for macrophytes (Jupp and Spence 1977). Furthermore, Vollenweider (1976) noted that increased growth of cladophora must be expected when the inflow concentration exceeds 40–50 $\mu g \cdot L^{-1}$. Therefore, it is logical that P control be directed to keeping the overall input concentration of P from rivers and point sources below that level, even when flows are low. Failure to maintain P control even for a few months in the summer for 1 or 2 yr of low runoff could prevent or retard the expected recovery process. The Bay has already responded quantitatively to reductions in P loading. The algal biomass has decreased (Nicholls et al. 1986) and P concentrations have decreased (Robinson 1986), and there are signs of a resurgence in the walleye stock (Hurley 1986). However, the Bay must be given time to recover, just as conditions took time to change from meso-oligotrophic to eutrophic (100+ yr) and from eutrophic to hypereutrophic in the upper Bay (10+ yr).

Conclusions

(1) Development in the nineteenth century changed the Bay of Quinte from an oligomesotrophic system supporting salmonids and coregonids to a eutrophic one, supporting percids and esocids. This change is not perceived as being entirely deleterious.

(2) Development after 1940 led to the upper Bay becoming hypereutrophic with an associated loss of valued fish stocks.

(3) Introduction of detergent controls and installation of tertiary treatment at 1 mg $P \cdot L^{-1}$ (0.5 in the summer time) effluent has prevented the worst excesses of hypereutrophication.

(4) Future management should be directed to keeping the summer input P concentration below 50 $mg \cdot m^{-3}$, even in low river flow conditions. The reduction in the final effluent to 0.5 mg $P \cdot L^{-1}$ will aid this effort considerably.

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References

CHAPRA, S. C. 1977. Total phosphorus model for the Great Lakes. J. Environ. Eng. Div., ASCE 103: 147–161.

1980. Simulation of recent and projected total phosphorus trends in Lake Ontario. J. Great Lakes Res. 6: 101–112.

CHRISTIE, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

DILLON, P. J. 1974. The prediction of phosphorus and chlorophyll concentrations in lakes. Ph.D. thesis, University of Toronto, Toronto, Ont.

DILLON, P. J., AND W. B. KIRCHNER. 1974. The effects of geology and land use on the export of phosphorus from watersheds. Water Res. 9: 135–148.

DILLON, P. J., AND F. H. RIGLER. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519–1531.

HURLEY, D. A. 1986. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

HURLEY, D. A., AND W. J. CHRISTIE. 1977. Depreciation of the warm water fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

INTERNATIONAL JOINT COMMISSION (IJC). 1978. Environmental management strategy for the Great Lakes system. Final Report to the IJC on Pollution from Land Use Activities Reference Group, IJC, Windsor, Ont.

JANUS, L. L., AND R. A. VOLLENWEIDER. 1981. Summary Report — The OECD Cooperative Programme on Eutrophication: Canadian contribution. IWD Sci. Ser. No. 131.

JOHNSON, M. G., J. COMEAU., W. C. SONZOGNI, T. HEIDTKE, AND B. STAHLBRAUM. 1978. Management information base and overview modelling. Report prepared for the Pollution from Land Use Activities Reference Group, IJC, Windsor, Ont.

JOHNSON, M. G., AND G. E. OWEN. 1971. The role of nutrients and their budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

JUPP, B. P., AND D. H. N. SPENCE. 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. J. Ecol. 65: 175–186.

MINNS, C. K., G. E. OWEN, AND M. G. JOHNSON. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

NICHOLLS, K. H., L. HEINTSCH, E. CARNEY, J. BEAVER AND D. MIDDLETON. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

ROBINSON, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

STOERMER, E. F., J. A. WOLIN, C. L. SCHELSKE AND D. J. CONLEY. 1985. Postsettlement diatom succession in the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. 42: 754–767.

TUCKER, A. 1948. The phytoplankton of the Bay of Quinte. Trans. Am. Microsc. Soc. 67: 365–383.

VOLLENWEIDER, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD Tech. Rep. Paris DAS/CSI/68, 27: 1–182.

1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53–83.

WARWICK, W. F. 1980. Paleolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 118 p.

A Simple Whole-Lake Phosphorus Model and a Trial Application to the Bay of Quinte

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Minns, C. K. 1986. A simple whole-lake phosphorus model and a trial application to the Bay of Quinte, p. 84–90. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

A simple whole-lake phosphorus model is presented. Coupled mass balance equations for the water column and surface sediment phosphorus pools in a lake are described. The model is shown to be a descendent of the Vollenweider (1969. Arch. Hydrobiol. 66: 1–36) model. The concept of "apparent settling velocity" is replaced with an operationally defined concept determined by sedimentation, reflux (internal loading), and permanent deposition rates. The model is used in an analysis of the Bay of Quinte phosphorus budgets. The dominance of internal loading is supported. The effect of uncertainty in key model parameters is shown. Use of the model for evaluation of lakes with changing phosphorus loads is recommended. Where reflux from the surface sediment pool is present, the response of lake water quality, as determined by phosphorus concentrations in the water column, will lag changes in external phosphorus loading rates. When external loading increases, the sediment pool retains phosphorus and minimizes the impact on water quality until it comes to steady state. When external loading decreases, the sediment pool delays the improvement in water quality because of reflux.

On présente un modèle simple de phosphore pour l'ensemble des lacs. On décrit les équations d'équilibre de masse appariées pour les réservoirs de phosphore se trouvant dans la colonne d'eau et dans les sédiments de surface d'un lac. On montre que le modèle est dérivé du modèle de Vollenweider (1969. Arch. Hydrobiol. 66 : 1–36). Le concept de «vitesse apparente de sédimentation» est remplacé par un concept défini opérationnellement qui est déterminé par la sédimentation, le reflux (charge interne) et les taux permanents de dépôt. On se sert du modèle pour procéder à une analyse des bilans de phosphore de la baie de Quinte. La dominance de la charge interne est étayée. On montre l'effet de l'incertitude sur les paramètres importants du modèle. On recommande l'utilisation du modèle pour évaluer les lacs où les quantités de phosphore varient. Quand il y a reflux à partir du réservoir des sédiments de surface, la qualité de l'eau du lac, telle que déterminée par les concentrations de phosphore dans la colonne d'eau, ne suivra pas les changements des taux de chargement externe de phosphore. Quand le chargement externe augmente, le réservoir de sédiments retient le phosphore et minimise les répercussions sur la qualité de l'eau jusqu'à ce qu'il devienne stable. Quand le chargement externe diminue, le réservoir de sédiments retarde l'amélioration de la qualité de l'eau en raison de reflux.

Introduction

Considerable success in the management of eutrophication has been made possible by the use of simple lake phosphorus (P) models (Vollenweider 1969; Dillon 1974) which only deal with an input–output analysis of P in the water column. Although there is ample evidence of the role of lake sediments as a source as well as a sink for P, there have been, as Nürnberg (1984) pointed out, few attempts to deal explicitly with P exchange between the water column and bottom sediments in a simple model. There are examples in the literature, e.g. Emery et al. (1973) (Lake Sammamish) and Larsen et al. (1979) (Lake Shagawa), where lakes have failed to respond in the manner predicted by the Vollenweider model, when external P loading was greatly reduced. Sediments as a source of P were implicated in both cited examples. Imboden (1974) developed a two-layer model of the epilimnion and hypolimnion in a lake. He recognized that recovery might be delayed by release from enriched sediments but did not pursue an analysis of the role of the hypolimnion sediment P release term in his model. Snodgrass and O'Melia (1975) further developed the idea of a two-layer model but did not allow directly for a release of nutrients from the sediments, only that their loss term from the water column can be negative.

Lorenzen (1973) presented a set of models which accounted for both the release and sedimentation of P in lakes. He followed this up with a trial application of his final model to Lake Washington (Lorenzen et al. 1976). Digiano and Snow (1977) presented another model involving gradient-driven exchange between water column and interstitial P. Dillon (1974) suggested such an approach, i.e. coupled equations to describe water column and sediment P dynamics. Here, a simpler model is proposed which includes a sediment P pool. The model is developed, compared with others, and applied to the Bay of Quinte. Finally, the implications of this approach to the study of P budgets in lakes are considered.

Earlier models relied on a term "net sedimentation" (Vollenweider 1975), i.e. the net balance of gross sedimentation and sediment release or reflux, to complete the mass balance equation for the water column of a lake. The lack of agreement between the earlier models and results usually arose from the requirement that gross sedimentation and reflux have a fixed relationship. This difficulty was usually overcome by addition of other factors or coefficients to the models. Vollenweider (1976) added a further component related to flushing, while Chapra (1982) made the net sedimentation coefficient a hyperbolic function of mean depth. An alternative approach is the use of two simultaneous equations, one for the water column and one

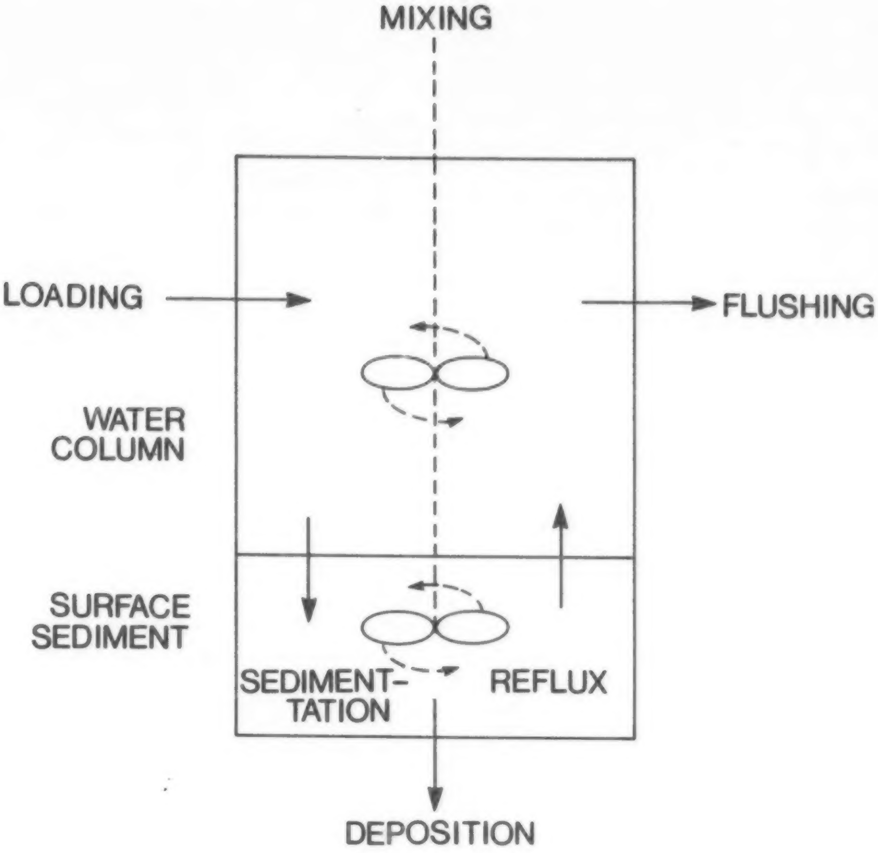

FIG. 1. Concept of a two-component whole-lake P model.

for the sediment pool.

The Model

The dynamics of P pools in the water column and surface sediments of a lake (Fig. 1) can be described by two equations (see Appendix for definition of symbols):

$$(1)\quad \dot{P}_w = L - \sigma P_w - \rho P_w + \gamma P_s$$
$$= \text{loading} - \text{sedimentation} - \text{flushing} + \text{reflux}$$

$$(2)\quad \dot{P}_s = \sigma P_w - \gamma P_s - \delta P_s$$
$$= \text{sedimentation} - \text{reflux} - \text{deposition.}$$

Loading comes from runoff, point sources, and the atmosphere. Sedimentation is that P which settles out of the water column into the surface sediments. Runoff replaces the water in the lake and removes P by flushing. Reflux is the release of nutrients by whatever mechanism (e.g. resuspension, diffusion, biotic migration) from the surface sediments into the water column. Below the mixed layer of surface sediments, there is a permanent accumulation of sediment (i.e. deposition) from which reflux is not possible. Incoming sediment continually renews the mixed layer, which then moves up to incorporate the new material and conserve its dimensions.

Chapra and Reckhow (1983, p. 389–390) presented a similar set of equations for the allochthonous solids budget of a lake. However, their equations were only an intermediate step in the derivation of a more elaborate model and they did not analyze the simpler model. In a similar model, Lorenzen et al. (1976) forced δP_s in equation (2) to be equal to σP_w times a constant. In the model of Digiano and Snow (1977) the reflux depends on the concentration gradient between water column P [P_w] and interstitial [P] and an adsorption equilibrium between [P_s] and interstitial [P]. They ignored deposition.

Equations (1) and (2) can be analyzed as follows. At steady state,

$$(3)\quad L - \sigma P_w - \rho P_w + \gamma P_s = 0$$

and

$$(4)\quad \sigma P_w - \gamma P_s - \delta P_s = 0.$$

Equation (4) can be rearranged to yield P_s as a function of P_w. This function can then be substituted into (3) and (3) rearranged to yield P_w as a function of L and the coefficients:

$$(5)\quad P_w = L/[\rho + \sigma\delta/(\gamma + \delta)].$$

This is the result obtained by Vollenweider (1969) except that σ is modified by the ratio $\delta/(\gamma + \delta)$.

Vollenweider (1969) proposed that the flux of P from the water column to the sediment be a proportion (σ) of the P in the water column. In a completely mixed system, this is the same as assuming that the P in the water column has a fixed settling rate (v, metres per year) such that σ equals $v/\overline{Z}$. This formulation has been used extensively (Imboden 1974; Chapra 1977; Dillon 1974). However, it was found (Vollenweider 1976) that settling rates estimated from P budgets were considerably less than those obtained by direct measurement. Thus, the term "apparent settling velocity" (v') arose. Equation (5) offers a resolution of this difficulty. When the reflux term, γ, is greater than zero, as is likely in most cases (Nurnberg 1984), the settling rate is modified by the ratio of deposition to reflux plus deposition.

Equation (5) can be further rearranged by substitution. If both sides are divided by the lake volume (V), Q/V is substituted for σ, and $v/\overline{Z}$ substituted for σ, the result is

(6) $$[P_w] = L_p/[q_s + v\delta/(\gamma + \delta)].$$

This is again a familiar equation where the lake P concentration is a function of the specific loading rate (L_p), the hydraulic load (q_s), and the settling rate (v) modified by $\delta/(\gamma + \delta)$. If on one hand the reflux (γ) is assumed to be zero, the equation reduces to that of Vollenweider (1969):

(7) $$[P_w] = L_p/[q_s + v].$$

On the other hand, as reflux increases, the ratio $\delta/(\gamma + \delta)$ tends towards zero, net retention of P in the sediments becomes negligible, and the lake concentration will equal the input concentration:

(8) $$[P_w] = L_p/q_s.$$

Of course, these are steady-state conditions. If, as we expect, the reflux is greater than zero, $[P_w]$ could violate the extremes of (7) and (8) given rapidly changing loading rates. If, over an interval, loading increased significantly, it is expected that the sediment pool would lag behind the water column in coming to a new steady state. In the interim, $[P_w]$ might fall below the limit predicted by (7). Vice versa, with a decrease in loading, the sediment pool would lag again and in the interim, $[P_w]$ might exceed the limit predicted by (8).

To realize the significance of these equations, it is necessary to know the expected values of the settling rate (v) and the hydraulic load (q_s). Imboden (1974) suggested that settling rates were in the range 0.1–0.4 $m \cdot d^{-1}$. Snodgrass and O'Melia (1975) suggested that v had a base rate of 0.05 $m \cdot d^{-1}$ which increased with the thickness of the lake layer according to the formula (1 + 0.05 times the layer thickness (metres)). So, for a layer of 10 m, the rate would be 0.075 $m \cdot d^{-1}$, while for a layer of 100 m the rate would be 0.3 $m \cdot d^{-1}$. Particles, detritus, and algae are expected to be the source of settling material. According to Smith (1975) a 1-μm-diameter cell, with a specific gravity close to unity, would sink $\simeq$0.001 $m \cdot d^{-1}$, a 10-μm cell $\simeq$0.086 $m \cdot d^{-1}$, and a 100-μm cell $\simeq$0.43 $m \cdot d^{-1}$. Burns and Rosa (1980) reported settling velocities for 10 species of phytoplankton ranging from 0.07 to 0.31 $m \cdot d^{-1}$. Reynolds (1984) reported rates of 0.2–1.2 $m \cdot d^{-1}$ for large nonmotile algae. Sprules et al. (1983) reported that most algae in 26 lakes were in the 5–20 μm range.

The settling rate (v) can be estimated from the ratio of measured sedimentation rates and the average concentration of P in the water column. Since it is only the downward flux (σP_w) that is of interest, it is important to correct for resuspended sediment in sediment trap catches (Charlton 1975). A number of literature sources contained sufficient data to calculate a settling rate (Table 1). The estimates averaged 0.113 ± 0.064 $m \cdot d^{-1}$ ($\overline{X}$ ± SD). This is equivalent to 40.9 ± 23.2 $m \cdot yr^{-1}$. For the rest of the analysis, I have assumed this is an estimate of v.

TABLE 1. Estimates of the settling rate (v) derived from P budget and sedimentation studies.

Location	Mean depth, $\overline{Z}$ (m)	Estimated settling rate, v ($m \cdot d^{-1}$)	Source
Lake Kinneret	25.0	0.19	Serruya 1975
Lake of Lucerne (Horwer Bay)	42.6	0.02	Bloesch 1974
Rotsee	9.0	0.03	Bloesch 1974
Lake Washington	32.9	0.15	Edmondson and Lehman 1981
Lake Norrviken	5.4	0.13	Ahlgren 1972
Bay of Quinte	9.7	0.16	Minns et al. 1986
Limnocorral	4.0	0.12	Charlton 1975
Mean ± SD		0.113 ± 0.064	

The average settling rate (v, 0.113 $m \cdot d^{-1}$) is comparable with those reported above for various particles. Phosphorus settling rates, corrected for reflux, should vary as the proportion of total P incorporated in particles varies. The net flux (sedimentation + reflux) between the water column and the sediment will vary seasonally with changes in the depth and intensity of mixing in the water column, which can cause resuspension of sediment P in particles, i.e. part of the reflux term in the model. However, the settling rate (v) is not affected by the mixing regime, unlike the net or apparent settling velocity. Vollenweider (1976) suggested that the apparent settling velocity (v') was about 10 $m \cdot yr^{-1}$. Chapra (1982) estimated that the maximum apparent settling velocity was 24.5 and that in individual lakes was a function $v' = v'_{max}(1 - \exp(-0.075\ \overline{Z}))$. It follows from the model development here that at steady state,

(9) $$v' = v \cdot \delta/(\delta + \gamma).$$

On a transient basis, v' can be negative.

It is usually considered that $q_s < v$ (Imboden 1974). Data presented by Turner et al. (1983) support this contention. Snodgrass and Dillon (1983) pointed out that the relative magnitudes of q_s and v (or v') are important in determining the source of variability in $[P_w]$. This is an important consideration with regard to the retention coefficient (R) and the ratio of internal to external loading (R_{IE}):

(10) $$R = \frac{v'}{q_s + v'} = \frac{v}{v + q_s(\gamma + \delta)/\delta}$$

(11) $$R_{IE} = \frac{\gamma P_s}{L} = \frac{\gamma}{\delta + q_s(\delta + \gamma)/v}.$$

As q_s/v increases, both R and R_{IE} decrease. Also of interest are the turnover times of the sediment and water column P pools:

(12) $$\tau_w = 1/[\rho + \sigma\delta/(\gamma + \delta)]$$

(13) $$\tau_s = 1/[\gamma + \delta].$$

A priori, it is expected that $\tau_s < \tau_w$.

Thus it is to be expected that lakes with a long history of nutrient enrichment will show a lagged recovery when nutrient loading is decreased because of P in the surface sediments (Schindler 1976). Examples of lagged recovery include Lake Norrviken (Ahlgren 1972), Shagawa Lake (Larsen et al. 1975),

TABLE 2. Phosphorus budget data for the Bay of Quinte.

Parameter	Period	Upper bay	Whole bay	Source
A_o (km^2)		136.4	257.4	Minns et al. 1986
$\overline{Z}$ (m)	1972–77	4.3	10.5	Minns et al. 1986
	1978–81	4.2	10.3	Minns et al. 1986
L_p (mg·m^{-2}·yr^{-1})	1967–77	2486 ± 500	2252 ± 610	
	1978–81	2254	2345	Minns et al. 1986
ρ	1967–77	11.8 ± 1.8	7.3 ± 2.0	Minns et al. 1986
	1978–81	12.9	12.1	Minns et al. 1986
Correlation L_p with ρ	1967–77	0.833	0.851	Minns et al. 1986
Mean [P_w] (mg·m^{-3})	1972–77	64.7	39.1	Minns et al. 1986
	1978–81	45.6	30.9	Minns et al. 1986
Mean $\gamma \cdot P_s$ (mg·m^{-2}·d^{-1})	1972–77	10.7	5.6	Minns et al. 1986
δP_s (mg·m^2·d^{-1})		1.35 (0.28–3.55)	1.54 (0.32–4.05)	Joshi and Fox 1985; Warwick 1980
ν' estimated from (9)		4.58 ± 2.61	8.83 ± 5.04	

the Bay of Quinte (Minns et al. 1986), and possibly Lake Washington (Edmondson and Lehman 1981).

Inclusion of the role of the sediments in predicting the recovery of lakes from excess P loading requires that the size of the active sediment pool (P_s), the deposition (δ), and the reflux (γ) coefficients be determined. There are a large number of studies where the flux rate (γP_s) has been estimated (Nürnberg 1984). With the advent of radionuclide methods, there have been many studies where long-term sediment deposition (δP_s) has been estimated (cf. Robbins 1982). The greatest difficulty lies in determining the size of the sediment pool (P_s). Robbins (1982) found that the mixed layer in the Great Lakes varied from 1 to 15 cm thick depending on the abundance and penetration of macrobenthos. In shallow situations, wave-induced sediment mixing is to be expected.

In steady-state situations, the ratio $\delta P_s / (\gamma P_s + \delta P_s)$ would suffice for using equation (6) to predict [P_w]. In situations where loading is changing, it is necessary to know the size of the pool (P_s).

Functionally, deposition is a burial process (Robbins 1982) and depends on the influx of new sediment from the watershed. So it is to be expected that the sediment load, and so deposition (δ), will be a function of the hydraulic load (q_s). This may explain, in part, why Vollenweider (1976) had some success in defining critical load with a function of σ involving q_s.

Trial Application to the Bay of Quinte

Application of this model to any situation requires that a number of parameters be estimated. If the situation involves evaluation of changing loads, it is essential that the size of the sediment pool be determined. If the object is to predict future P concentrations, some measure of uncertainty will be needed. Reckhow and Chapra (1983) suggested the use of first-order error analysis as a starting point.

The Bay of Quinte is a large eutrophic bay at the eastern end of Lake Ontario. Since 1972, it has been the subject of an intensive study to assess its response to P management. Minns et al. (1986) have described the P loadings and budgets for the period 1965–81. The bay was treated in three parts: upper, middle, and lower. There is a large drainage area and the upper bay has a high flushing rate (11.8 ± 1.8·yr^{-1}). The middle and lower bay sections have exchange flows with Lake Ontario and so the whole bay also has a high flushing rate (7.3 ± 2.0·yr^{-1}). The upper bay is shallow (Z = 4.3 m, 1972–77), while the lower bay is deep, giving the whole bay a mean depth of 10.5 m (1972–77). The budget analyses indicated that internal P loading dominated. In many years the upper bay exported more P than was imported. The sediments in the accumulation zones are highly enriched with P (1.494 mg·g^{-1} in 1972, R. L. Thomas, IJC, Windsor, Ont., pers. comm.). Prior to 1972, point-source P loadings were as high as 300 kg·d^{-1}. During the period 1972–77, the loadings were about 200 kg·d^{-1}. After installation of new treatment facilities in the winter of 1977–78, the loadings were about 80 kg·d^{-1}. The prognosis was that until the internal loading dissipated (i.e. sediment P concentrations declined), the full effect of external P controls would not be realized.

Initially, it is instructive to calculate the expected steady state using data for the period 1972–77. Most of the data needed (Table 2) are drawn from Minns et al. (1986). The main unknown is the value of ν' or $\nu\delta / (\delta + \gamma)$. Minns et al. (1986) estimated the sediment reflux (γP_s) for 1972–77 by back-calculation with P budgets. Joshi and Fox (1985) and Warwick (1980) have presented estimates of sediment deposition based on three and one cores, respectively, at points throughout the bay. They estimated sediment deposition at points in accumulation zones using radionuclide dating techniques. The rates ranged from 0.020 to 0.254 g·cm^{-2}·yr^{-1} with a mean of 0.0965. Combined with estimates of the extent of the accumulation zone (34.1% in the upper bay, 39.0% for the whole bay) and the average P content of surface sediment (1.494 mg·g^{-1}) provided by R. L. Thomas (pers. comm.), the deposition of P (δP_s) can be estimated: 1.35 mg P·m^{-2}·yr^{-1} (range 0.28–3.55) in the upper bay and 1.54 (range 0.32–4.05) in the whole bay.

As a cross-check, the sediment deposition can also be estimated from the sediment load, i.e. the suspended solids load. From data in Ongley (1973), the mean suspended solids concentration of runoff entering the Bay of Quinte was estimated to be 11.49 g·m^{-3}. Using the flushing data for the upper bay, the annual sediment deposition is 0.1710 ± 0.026 g·cm^{-2}·yr^{-1} in the accumulation zone. Applied to the whole bay's accumulation zone, the deposition is 0.0792 ± 0.0121 g·cm^{-2}·yr^{-1}. The presumption is that the sediment load to the upper bay is not retained there but replaces sediment being transported to the lower bay and out into Lake Ontario. Damiani and Thomas (1974) showed that the upper bay sediments are lacking in very

TABLE 3. Steady-state predictions of $[P_w]$ ($\mu g \cdot l^{-1}$) for the Bay of Quinte, 1972–77 and 1978–81 (standard deviations estimated using first-order error analysis).

Predictor	Upper bay	Whole bay
Observed mean (1972–77)	64.7	39.1
Predicted		
L_p/q_s (8)	49.0 ± 14.6	29.4 ± 13.5
$L_p/[q_s + v\delta/(\delta + \gamma)]$ (6)	44.9 ± 13.1	26.3 ± 11.6
$L_p/[q_s + v]$ (7)	27.1 ± 9.7	19.2 ± 8.26
Observed mean (1978–81)	45.6	30.9
Predicted		
Equation (8)	41.6	18.8
Equation (6)	38.4	17.6
Equation (7)	23.7	14.2

fine particles, which indicates (R. L. Thomas, pers. comm.) a disequilibrium between input and output. Overall, however, the sedimentation value of 0.0965 $g \cdot cm^{-2} \cdot yr^{-2}$ derived above does not appear unreasonable.

The calculation of standard error below used in first-order error analysis involves only the contribution of standard deviations of L_p, q_s, and v. A single value of $\delta/(\delta + \gamma)$ was calculated for the upper bay (0.112) and the whole bay (0.216). Assuming that v' is uncorrelated with L_p and q_s, the expected steady-state values of $[P_w]$ can be calculated for equations (6), (7), and (8). The predictions (Table 3), despite wide confidence intervals, do not encompass the observed mean for the period 1972–77. As expected, the Bay of Quinte does not appear to be close to a steady state. The decline in internal loading is lagging changes in external loading.

Given that the bay appears not to be near steady state, it is obviously of interest to estimate the recovery time from the 1972–77 state. This requires that the size of the active sediment pool be known. Joshi and Fox (1985) found there was evidence of considerable sediment mixing in the three cores they analyzed. The caesium profiles indicated mixing down to 8–10 cm. The ^{210}Pb profiles were inconsistent and probably did not go deep enough to reveal the mixed layer. Warwick's (1980) core showed a mixed layer of only 2–3 cm based on a ^{210}Pb profile. O. Johannsson (GLFRB, pers. comm.) has found chironomids as deep as 25 cm in the sediments of the accumulation zone in the upper bay. According to Robbins (1982), that depth would approximate the mixed depth. The available data are not sufficient to firmly establish the mixed depth.

Given the uncertainty regarding the size of the sediment pool, it seems best to examine how sensitive model predictions are to a range of depths. Taking the average conditions described above and three thicknesses of sediment layer, the results (Table 4) show that while the steady-state concentrations are unaffected, the sediment pool turnover time (13) increases with increasing thickness. The equations predict a dramatic increase in $[P_s]$ from 1.494 $mg \cdot g^{-1}$ (the 1972 value) to 0.619 to 0.625. Analysis of limited sampling ($N = 12$) of surface sediments in the upper bay in 1977 showed a mean of 1.119 $mg \cdot g^{-1}$ (C. K. Minns, unpubl. data). Based on 1972–77 loadings, the predicted steady state of $[P_w]$ was 44.9 $\mu g \cdot l^{-1}$ for the upper bay and 26.3 for the whole bay. After 1977, point-source loadings decreased and the observed P concentrations declined (Table 2). Of course, with lower loadings, for a given q_s, the steady-state predictions (1978–81) also decrease (Table 3). The recovery is lagging even after 4 yr. So, the turnover time (τ_s) must be relatively long and therefore the thickness of the mixed sediment layer must be relatively high.

The next stage in the application of the model to the Bay of Quinte will require (i) that a series of sediment cores be dated using ^{210}Pb to establish the thickness of the mixed layer and the mean and standard deviation of deposition rates and (ii) that a subset of the surface sediment survey conducted by R. L. Thomas in 1972 be repeated to look for changes in the sediment P concentration.

Clearly the Bay of Quinte is not near to a steady state with respect to P loading. This implies that if current P control strategies are kept in place, further improvements in water quality can be expected in the future.

Discussion

This simple model (equations (1) and (2)) has a number of advantages over its immediate ancestor, the Vollenweider (1969) model. The model has a complete accounting of the input and output of P for a lake. Inclusion of a sediment pool facilitates an explanation of the lagged response to P control encountered in systems with long enrichment histories. It offers a substitute for the concept of apparent settling velocity. This, in turn, allows for a wider range of retention values (R) depending on the relative size of the γ and δ coefficients.

The model is useful in that it focusses more attention on P reflux from sediments. The value of γ and how it varies with lake and loading characteristics is of great importance in determining the effectiveness of P control strategies. As Lorenzen et al. (1976) showed with a similar model, if γ is greater than zero, recovery will be retarded. In the treatment here, it has been assumed that γ is a constant. If γ increased with rising $[P_s]$, the decline in water quality due to increasing loading would be delayed but would be ultimately relatively worse than if γ were a constant.

Replacement of the apparent settling velocity concept with one that separates sedimentation and reflux allows a better understanding of the retention coefficient (R). As loading decreases, retention will decrease for some time, but will eventually return to similar levels, as was observed in Lake Washington (Edmondson and Lehman 1981).

No attempt has been made to further interpret the mechanism of sediment reflux. Whether it is due to diffusion, resuspension, or biotic transport is not critical to this analysis. It is more important that the fluxes of sedimentation, reflux, and deposition be considered separately in the evaluation of lake P dynamics. The relative magnitude of these fluxes can greatly affect a lake's response to P management.

The trial application of the model to the Bay of Quinte illustrates the difficulties to be encountered in situations where loading is changing. However, the model does lead to a useful integration of information and provides direction for future research. The prognosis is that improvements in water quality can be expected in the future with no further decreases in point-source P loading.

This model incorporates the effect of sediment deposition and reflux on the dynamics of P in the water column of a lake. If all parameters can be estimated, prediction of a lake's response to changing loading should be relatively simple. It is recommended that this successor to the Vollenweider model be used to assess the response of lakes to P loading management.

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TABLE 4. Turnover time and steady-state predictions with a range of mixed sediment layer depths.

	Upper bay		Whole bay
Initial Conditions			
P_w (kg)	37889.7		105182.0
L ($kg \cdot yr^{-1}$)	339090.4		579664.8
ρ (yr^{-1})	11.8		7.3
σ (yr^{-1}) ($v/\overline{\overline{Z}}$)	9.5		3.9
$[P_s]$ ($mg \cdot g^{-1}$) (1972)		1.494	
γP ($kg \cdot yr^{-1}$) (1972–77)	530564.0		525235.0
Sediment Assumptions			
Water content of mixed layer (%)		90	Joshi and Fox 1985
Sediment solids density ($g \cdot cm^{-3}$)		2.45	Joshi and Fox 1985
Sediment input ($g \cdot cm^{-2} \cdot yr^{-1}$)		0.0965	See text

	Thickness of mixed layer (cm)					
	10	20	30	10	20	30
P_s (kg)	1702493	3404986	5107479	3674429	7348858	11023287
γ	0.3120	0.1560	0.1040	0.1430	0.0710	0.0480
δ	0.0394	0.0197	0.0131	0.0394	0.0197	0.0131
τ_w (yr)	0.08	0.08	0.08	0.12	0.12	0.12
τ_s (yr)	2.85	5.69	8.54	5.48	11.03	16.37
$[P_w]$ ($mg \cdot m^{-3}$)	44.9	44.9	44.9	26.3	26.3	26.3
$[P_s]$ ($mg \cdot g^{-1}$)	0.625	0.625	0.625	0.619	0.619	0.619

thank the Project Quinte group for their support and critical reviews. I also wish to thank the three anonymous reviewers for their comments and suggestions.

References

AHLGREN, I. 1972. Changes in Lake Norrviken after sewage diversion. Verh. Int. Ver. Limnol. 18: 355–361.

BLOESCH, J. 1974. Sedimentation und Phosphorhaushalt im Vierwaldstättersee (Horwer Bucht) und im Rotsee. Schweiz. Z. Hydrol. 36(1): 71–186.

BURNS, N. M., AND F. ROSA. 1980. In situ measurement of the settling velocity of organic carbon particles and 10 species of phytoplankton. Limnol. Oceanogr. 25(5): 855–864.

CHAPRA, S. C. 1977. Total phosphorus model for the Great Lakes. J. Environ. Eng. (ASCE) 103(EE2): 147–161.

1982. A budget model accounting for the positional availability of phosphorus in lakes. Water Res. 16: 205–209.

CHAPRA, S. C., AND K. H. RECKHOW. 1983. Engineering approaches for lake management. Volume 2: Mechanistic modelling. Butterworths, Wellington, New Zealand. 492 p.

CHARLTON, M. N. 1975. Sedimentation: measurements in experimental enclosures. Verh. Int. Ver. Limnol. 19: 267–272.

DAMIANI, V., AND R. L. THOMAS. 1974. The surficial sediments of the Big Bay section of the Bay of Quinte, Lake Ontario. Can. J. Earth Sci. 11: 1562–1576.

DIGIANO, F. A., AND P. D. SNOW. 1977. Consideration of phosphorus release from sediments in a lake model, p. 318–323. *In* H.L. Golterman [ed.] Interaction between sediments and freshwater. Dr. W. Junk Publishers, The Hague.

DILLON, P. J. 1974. A critical review of Vollenweider's nutrient budget model and other related models. Water Res. Bull. 10(5): 969–989.

EDMONDSON, W. T., AND J. T. LEHMAN. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnol. Oceanogr. 26(1): 1–29.

EMERY, R. M., C. E. MOON, AND E. B. WELCH. 1973. Recovery of a mesotrophic lake after nutrient diversion. J. Water Pollut. Control Fed. 45: 913–925.

IMBODEN, D. M. 1974. Phosphorus model of lake eutrophication. Limnol. Oceanogr. 19(2): 297–304.

JOSHI, S. R., AND M. E. FOX. 1985. The ^{210}Pb and ^{137}Cs profiles in sediment cores from Bay of Quinte, Lake Ontario. J. Radioanal. Nucl. Chem. 90: 207–215.

LARSEN, D. P., K. W. MALUEG, D. W. SCHULTS, AND R. M. BRICE. 1975. Response of eutrophic Shagawa Lake, Minnesota, U.S.A., to point-source phosphorus reduction. Verh. Int. Ver. Limnol. 19: 884–892.

LARSEN, D. P., J. VAN SICKLE, K. W. MALUEG, AND P. SMITH. 1979. The effect of wastewater phosphorus removed on Shagawa Lake, Minnesota: phosphorus supplies, lake phosphorus and chlorophyll 'a'. Water Res. 13: 1259–1272.

LORENZEN, M. W. 1973. Predicting the effects of nutrient diversion on lake recovery, p. 205–210. *In* E. J. Middlebrooks, D. H. Falkenborg, and T. E. Maloney [ed.] Modelling and eutrophication process. Ann Arbor Science Publishers, Ann Arbor, MI.

LORENZEN, M. W., D. J. SMITH, AND L. KIMMEL. 1976. A long term phosphorus model for lakes: application to Lake Washington, p. 75–91. *In* R. P. Canale [ed.] Modelling biochemical processes in aquatic ecosystems. Ann Arbor Science Publishers, Ann Arbor, MI.

MINNS, C. K., G. E. OWEN, AND M. G. JOHNSON. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

NÜRNBERG, G. K. 1984. The prediction of internal phosphorus load in lakes with anoxic hypolimnia. Limnol. Oceanogr. 29: 111–124.

ONGLEY, E. D. 1973. Sediment discharge from Canadian basins into Lake Ontario. Can. J. Earth Sci. 10: 146–156.

RECKHOW, K. H., AND S. C. CHAPRA. 1983. Engineering approaches for lake management. Volume 1: Data analysis and empirical modelling. Butterworths, Wellington, New Zealand. 340 p.

REYNOLDS, C. S. 1984. Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshwater Biol. 14: 111–142.

ROBBINS, J. A. 1982. Stratigraphic and dynamic effects of sediment reworking by Great Lakes zoobenthos. Hydrobiologia 92: 611–622.

SCHINDLER, D. W. 1976. Biogeochemical evolution of phosphorus limitation in nutrient-enriched lakes of the Precambrian Shield, p. 647–664. *In* J. O. Nriagu [ed.] Environmental biogeochemistry. Vol. 2. Metals transfer and ecological mass balances. Ann Arbor Science Publishers, Ann Arbor, MI.

SERRUYA, C. 1975. Nitrogen and phosphorus balances and load–biomass relationship in Lake Kinneret (Israel). Verh. Int. Ver. Limnol. 19: 1357–1369.

SMITH, I. R. 1975. Turbulence in lakes and rivers. Freshwater Biol. Assoc. Sci. Publ. No. 29: 79 p.

SNODGRASS, W. J., AND P. J. DILLON. 1983. A test of two models of different levels of complexity for predicting changes of phosphorus concentration in a lake's outflow. Ecol. Model. 19: 163–187.

SNODGRASS, W. J., AND C. R. O'MELIA. 1975. Predictive model for phosphorus in lakes. Environ. Sci. Technol. 9(10): 937–944.

SPRULES, W. G., J. M. CASSELMAN, AND B. J. SHUTER. 1983. Size distribution of pelagic particles in lakes. Can. J. Fish. Aquat. Sci. 40: 1761–1769.

TURNER, R. R., E. A. LAWS, AND R. C. HARRISS. 1983. Nutrient retention and transformation in relation to hydraulic flushing rate in a small impoundment. Freshwater Biol. 13: 113–127.

VOLLENWEIDER, R. A. 1969. Moglichkeiten und Grenzen elementarer Modelle der Stoffbilanz von Seen. Arch. Hydrobiol. 66: 1–36.

1975. Input–output models with special reference to the phosphorus loading concept in limnology. Schweiz. Z. Hydrol. 37: 53–84.

1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53–83.

WARWICK, W. F. 1980. Palaeolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 118 p.

Appendix: Symbols

P_w	Total amount of P in the water column (kg)
P_s	Total amount of P in the mixed surface sediment layer (kg)
$[P_w]$	Concentration of P in the water column ($mg \cdot m^{-3}$)
$[P_s]$	Concentration of P in surface sediment ($mg \cdot g^{-1}$)
σ	Sedimentation coefficient, $v/\overline{Z}$ (yr^{-1})
ρ	Flushing coefficient, Q/V (yr^{-1})
δ	Deposition coefficient (yr^{-1})
γ	Reflux coefficient (yr^{-1})
V	Lake volume ($10^6 m^3$)
A_o	Lake area (km^2)
$\overline{Z}$	Mean depth, v/A_o (m)
L	External loading ($kg \cdot yr^{-1}$)
L_p	Specific surface loading, L/A_o ($mg \cdot m^{-2} \cdot yr^{-1}$)
q_s	Hydraulic load, Q/A_o ($m \cdot yr^{-1}$)
Q	Total yearly water discharge
v	Settling velocity ($m \cdot yr^{-1}$)
τ_s	Turnover time, sediment
τ_w	Turnover time, water
R	Retention coefficient
R_{IE}	Ratio internal to external loading

Seasonal Trends in Turnover Times of Orthophosphate in the Bay of Quinte, Lake Ontario

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Millard, E. S. 1986. Seasonal trends in turnover times of orthophosphate in the Bay of Quinte, Lake Ontario, p. 91–99. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Orthophosphate turnover times were measured weekly throughout the Bay of Quinte, Lake Ontario, from May through September. The longest turnover times were in May but decreased to 5 min at some stations by early July. At this time, uptake was dominated by bacteria-size particles (0.45–1 μm) in the middle and lower bay as well as nannoplankton (1–8 μm) in the upper bay. Several factors suggested that the seston was phosphorus starved at this time. Total phosphorus, chlorophyll a, turnover times, and phosphorus uptake by larger particles (> 8 μm) increased by August, indicating that phosphorus supply had increased. Turnover times were fastest in the middle and lower bay when thermal stratification occurred. The shallow, fully mixed upper bay stations that were close to high point-source phosphorus loadings had long turnover times most frequently. The highest frequency of rapid turnover times occurred in the middle bay where the distance from point-sources of phosphorus and strong thermal stratification lowered available phosphorus supply.

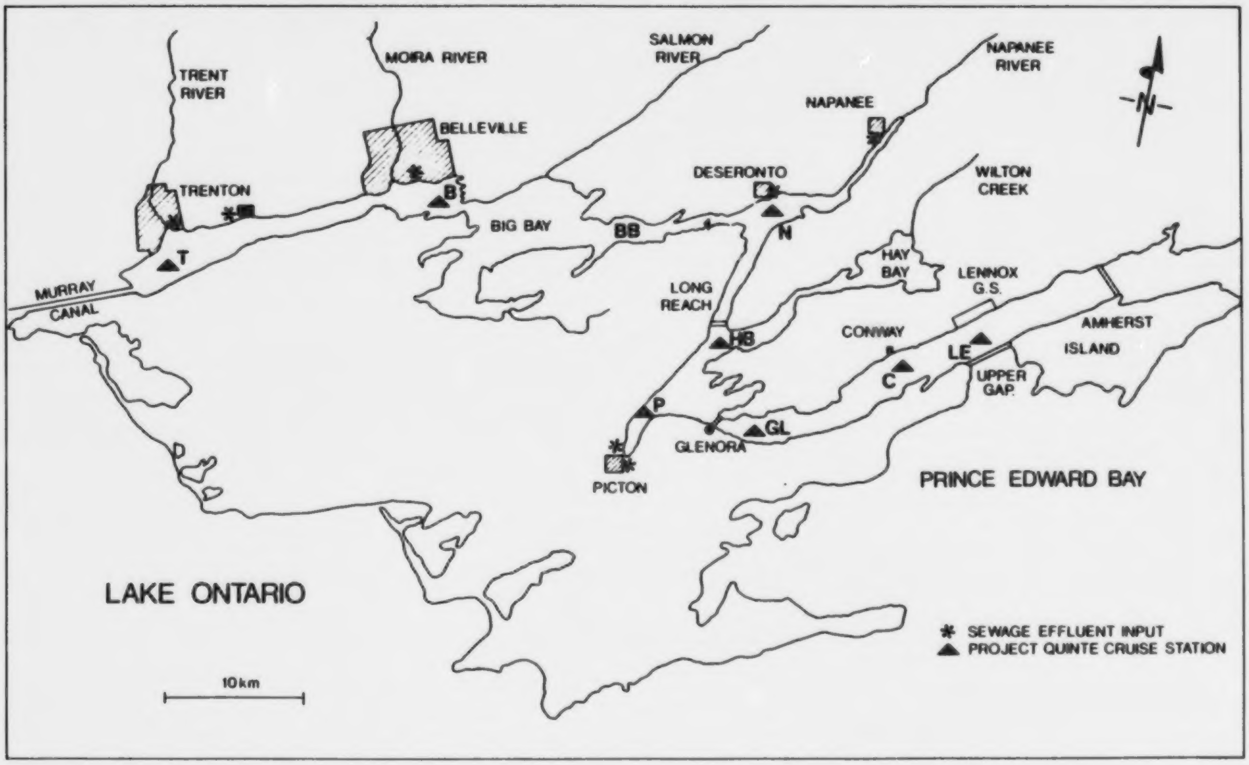
Le temps d'élimination des orthophosphates a été mesuré chaque semaine, de mai` septembre, dans toute la baie de Quinte sur le lac Ontario. Le temps le plus long a été observé en mai, mais, à certaines stations, il diminuait à cinq minutes au début de juillet. À cette époque, l'absorption dans la baie était surtout due à des particules de la taille des bactéries (0,45–1 μm) dans les parties centrale et inférieure, ainsi qu'au nannoplancton (1–8 μm) dans la partie supérieure. Plusieurs facteurs semblent indiquer que le seston disposait alors d'une quantité insuffisante de phosphore. Au mois d'août, l'apport de phosphore augmentait comme le montre l'accroissement du phosphore total, de la teneur en chlorophylle *a*, du temps d'élimination et de la quantité de phosphore fixé par les particules plus grosses (8 μm). En période de stratification thermique, l'élimination était la plus rapide dans les parties inférieure et centrale de la baie. Aux stations situées dans la partie supérieure, près de fortes sources ponctuelles de phosphore, où les eaux étaient peu profondes et homogènes, l'élimination était très souvent lente. C'est dans la partie centrale de la baie, loin des sources ponctuelles de phosphore, où une stratification thermique importante atténuait l'apport de cet élément, que l'élimination était le plus souvent rapide.

Introduction

The high summer phytoplankton biomass in the upper Bay of Quinte prior to phosphorus controls at sewage treatment plants was due to high point-source phosphorus loadings and low flushing rates (Johnson and Owen 1971; Minns et al. 1986; Millard and Johnson 1986). However, it was unclear when phosphorus controls were proposed (Johnson and Hurley 1986) whether proposed reductions were sufficient to limit algal growth and reduce standing crops. The purpose of this study was to assess the phosphorus demand of the phytoplankton throughout the Bay of Quinte, Lake Ontario, through frequent measurement of orthophosphate (PO_4) turnover time. The basic hypothesis was that determining seasonal trends in phosphorus demand could help determine the seasonal importance of phosphorus supply and thus the role of phosphorus controls relative to other growth factors.

Orthophosphate turnover time has been proposed as an index of phosphorus demand by the seston because it integrates the effects of available phosphorus, biomass of organisms, and cellular phosphorus content (Lean and Nalewajko 1979). Turnover time is the time required by the seston to take up an amount of PO_4 equal to the total pool of PO_4 in the water (Riggs 1967). Rapid turnover times indicate a high demand for PO_4 because phytoplankton biomass is high or PO_4 supply is low (Rigler 1956; Levine and Schindler 1980). In contrast, slow turnover times indicate low biomass, adequate PO_4 supply, or limitation of algal growth by some other factor (Rigler 1966; Peters 1974; Lean and Nalewajko 1979; White et al. 1982). Phosphate turnover time has been used by others to assess phosphorus limitation on a seasonal basis in an ultraoligotrophic lake (Chow-Fraser and Duthie 1983), in a comparison between an oligotrophic and eutrophic shield lake (Levine and Schindler, 1980), and in the eastern and central basins in Lake Erie (Lean et al. 1983).

Lean and Nalewajko (1979) improved the use of turnover time in assessing phosphorus demand by proposing that the shape of the curve showing loss of $^{32}PO_4$ from the filtrate could help describe the degree of demand. They identified three types of curves: type 1 where uptake is log-linear during the first hour, type 2 where a steeper log-linear slope bends to an asymptote, and type 3 where two log-linear lines fit the data after the asymptote is subtracted. Type 1 curves indicate low phosphorus demand and type 2 high demand, and type 3 curves indicate extreme phosphorus depletion and occur rarely. A combination of turnover time and curve type was used in this study to assess the seasonal trend in phosphorus demand. In addition, fractionation of $^{32}PO_4$ uptake was done to determine the changes in the importance of bacteria, nanno-, and net-phytoplankton to phosphorus demand during the season.


TRENT RIVER
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BIG BAY
BB
N
T
HAY BAY
LENNOX G.S.
MURRAY CANAL
LONG REACH
HB
CONWAY
AMHERST ISLAND
LE
C
UPPER GAP
P
GL
GLENORA
PICTON
PRINCE EDWARD BAY
LAKE ONTARIO
✱ SEWAGE EFFLUENT INPUT
▲ PROJECT QUINTE CRUISE STATION
10km

FIG. 1. Bay of Quinte and sampling locations; upper bay stations at T, B, BB, and N, middle bay stations are HB and P, and lower bay stations are GL, C, and LE.

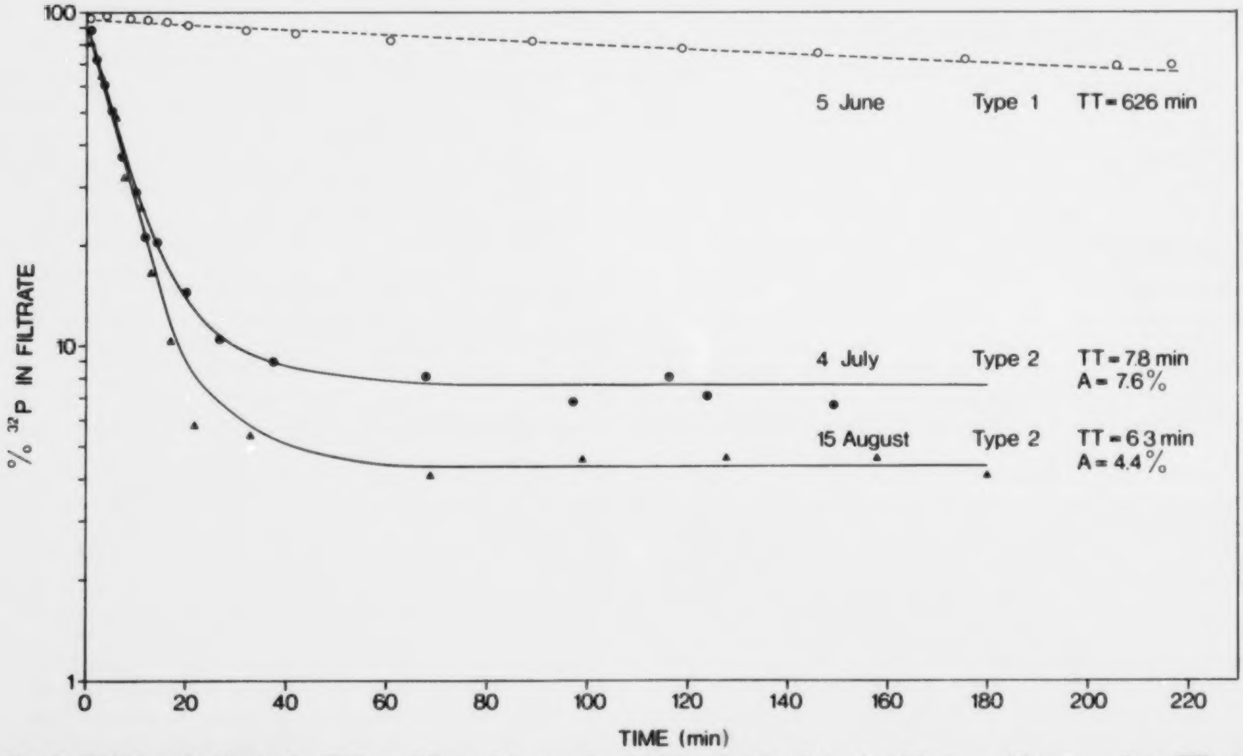

FIG. 2. Typical uptake kinetics for $^{32}PO_4$ on different dates at station N giving examples of type 1 and 2 curves with turnover times (TT) and asymptote levels (A).

Materials and Methods

Composite, euphotic zone water samples for phosphate uptake experiments were collected weekly from nine stations from 8 May to 26 September 1978 (Fig. 1). The sampling schedule coincided with weekly Project Quinte sampling cruises (Millard and Johnson 1986). Samples were transported to the laboratory and experiments started within at least 3 h of sampling.

Incubation temperatures were always kept at ± 1°C of the 1-m ambient temperature for the upper bay stations (T, B, BB, N) and for all other stations after the end of June. However, during May and June, ambient temperatures differed by up to 7°C between the middle (HB) and lower bay (P, GL, C, LE) stations that were all sampled on the same day. However, temperature difference was less (2–3°C) among the lower bay stations. As a result, samples were incubated 2–4°C below ambient for station HB and 1–2°C above for the lower bay in May and June.

Carrier-free $^{32}PO_4$ (Amersham) was added to a 0.5-L sample in a chromic acid washed plastic bottle to give a total activity of 10 000–15 000 $dpm \cdot mL^{-1}$. Aliquots (5 mL) were filtered through 24-mm, 0.45-μm cellulose–nitrate filters (Sartorius) and then rinsed with about 1 mL of distilled water. Examples of typical filtering frequency curve type and length of experiments are presented in Fig. 2. Filters plus rinse water were collected and the radioactivity determined by counting the Cerenkov radiation (Brown 1971) on a Beckman LS8100 liquid scintillation counter. The percentage of the initial tracer left in solution was calculated and plotted semilogarithmically versus time. The initial slope of this relationship approximates the rate constant for orthophosphate uptake and the reciprocal is the orthophosphate turnover time in minutes. When an asymptote was reached, curve-splitting techniques were used to determine the initial slope (Riggs 1967). All slopes were calculated by simple linear regression. Except for the distilled water rinse of filters, the procedure and treatment of data followed that outlined by Lean and Rigler (1974) and Lean and Nalewajko (1979). Any effect of the rinse would have probably been to consistently increase the amount of tracer in the filtrate. This could have occurred through lysis of delicate organisms, but this seems unlikely because of the brief exposure time of about 1 s. Alternately, washing of radioactivity in the water retained by the filter into the filtrate could have occurred (Lean and Burnison 1979). A consistently small increase of filtrate activity was unlikely to have significantly altered the calculation of the initital slopes. Parallel experiments with and without filtered lake water rinses have shown no effect on calculated turnover times (D. Lean, Environment Canada, pers. comm.).

Fractionation of total $^{32}PO_4$ uptake into different size categories was done weekly at stations B, N, HB, GL, and C. Fractionation was carried out at the end of each experiment when either isotopic equilibrium between the dissolved fraction and the seston had been reached, or in the case of experiments with slower uptake, after 3–5 h. Aliquots (15 mL) were filtered through 0.45-μm membrane filters (total $^{32}PO_4$ uptake by the seston) as well as 1- and 8-μm Nuclepore filters. These filters were used because of the inadequacy of membrane filters for particle size fractionation (Burnison 1975). Aliquots were also passed through 64-μm nylon meshes before filtration through 0.45-μm membrane filters. The proportion of the total $^{32}PO_4$ uptake by each size category (i.e. 0.45–1 μm) was calculated from the difference between the activities retained. Filters were counted because most of the tracer was usually in the seston at the time of fractionation. All filters were counted with PCS fluor (Amersham) to increase efficiency and quench-corrected using the sample channels, ratio method.

Composite, euphotic zone samples for chlorophyll *a* were collected at the same time as those for phosphorus uptake and filtered through GFC filters (Whatman Co.) (Millard and Johnson 1986). Filters were frozen and later analyzed by the Water Quality Branch, Canada Centre for Inland Waters, Burlington (Environment Canada 1979). Samples for total phosphorus were collected on the weekly Project Quinte sampling cruises within 1–2 h of collections for tracer experiments (Robinson 1986). Mixing depths and thermal stability, the latter characterized by the solution (N^2) of the Brunt–Väsälä equation (Phillips 1966), were determined from vertical profiles of density (Millard 1986).

Results

$^{32}PO_4$ Turnover Times

Turnover times for $^{32}PO_4$ were slow (130–1800 min) at all stations from early May until late June (Fig. 3). Turnover times started to decline on 20 June from station N lakeward to LE (7.5–21.6 min) and remained low until 18 July. Turnover times during this period were the most rapid of the study, with many values < 10 min. An exception was the week of 26 June when very long turnover times (246–1552 min) occurred at these stations. Turnover times also decreased at stations T, B, and BB by late June but were not usually as rapid. However, a minimum turnover time for the study of 2.5 min, indicating extreme phosphorus demand, was measured at station T on 26 June and turnover time was only 12.7 min on 10 July at station B. Station BB had the longest minimum July turnover time of all locations (36 min). From late July to early August, turnover times increased to over 100 min on at least one occasion at all stations except HB. Unlike other stations, turnover times from mid- to late August were short at stations N and HB (6.3–15.4 min). Except for isolated dates at stations B (9 August, turnover time = 10.6 min) and T (4 September, turnover time = 16.8 min), turnover times were not under 20 min during August and September at any other stations. The average September turnover time was 100 min at all stations except T and N where the averages were 41 and 46 min, respectively.

Curve Type

Examples of type 1 and 2 curves found at station N during this study are presented in Fig. 2. The type 2 curves show differences in asymptotes as turnover time decreases. Type 1 curves were common in this study and occurred at all stations from early May until late June. Type 2 curves occurred from station HB down to LE from 19 June to 17 July when turnover times were shortest. During this same period, type 2 curves occurred at station N on the two dates when turnover times were < 10 min. Stations T and B had type 2 curves only twice during the study, while BB had neither a curve of this type nor a turnover time of < 20 min. Type 2 curves were most frequent at station HB. From late July until the end of September, type 1 curves occurred on all dates at all stations except N and HB. These stations had type 2 curves on three consecutive dates in August when turnover times were rapid.

Asymptote levels in midsummer in small lakes when phosphorus kinetics are usually most rapid are typically 1–5% (Rigler 1964). In this study, asymptotes were usually slightly higher at 5–10%. On some occasions, the criterion for a type 1 curve, log-linear loss of $^{32}PO_4$ from the filtrate for 60 min was

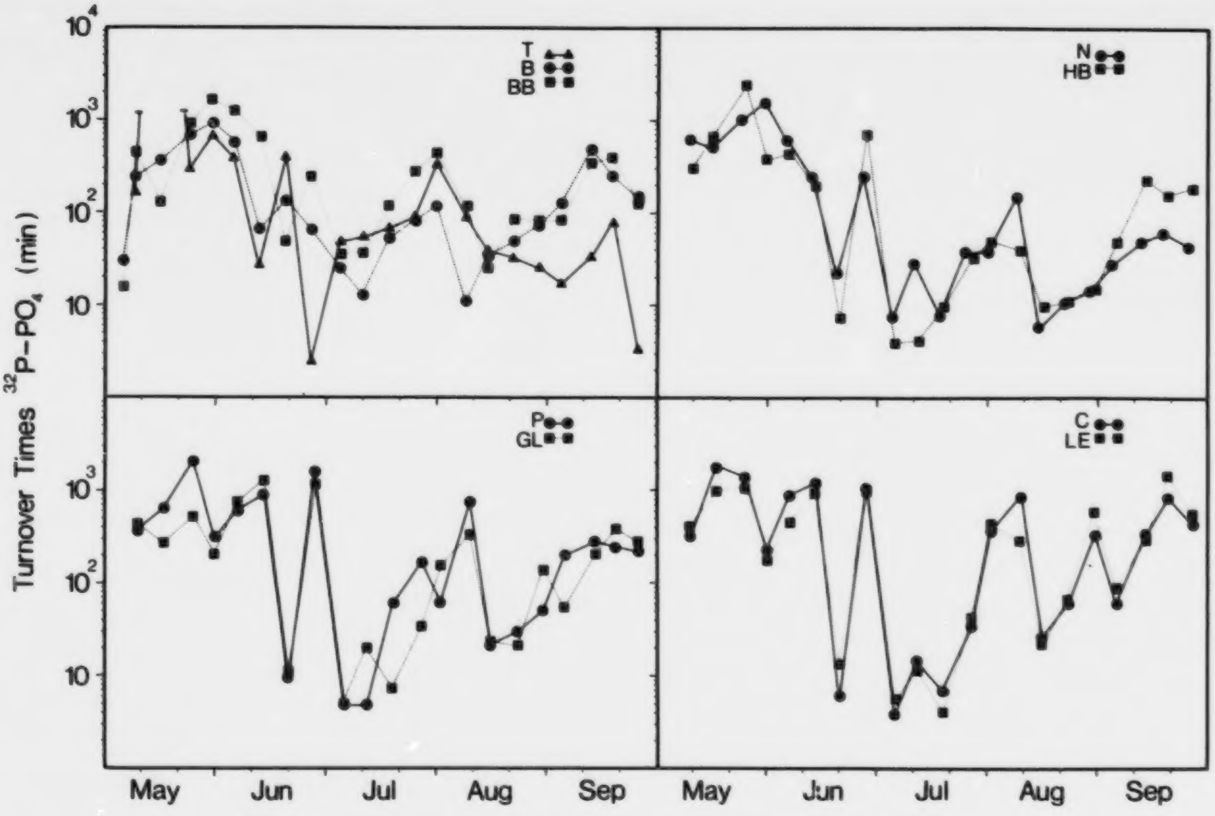

FIG. 3. Seasonal trends in $^{32}PO_4$ turnover times at all stations in the Bay of Quinte.

met, but an asymptote as low as 3.5% was eventually reached. Higher asymptotes have been found by Peters (1975) in European lakes (22–70%) and by Nalewajko and Lee (1981) in Lake Superior (21–26%). Decline in asymptote level may reflect an increase in phosphorus demand due to high biomass or decrease in phosphorus supply. Nalewajko and Lee found that levels dropped in September when turnover times were shorter and increased when phosphate was added in enrichment experiments.

Uptake of $^{32}PO_4$ by Size Categories

Fractionation of $^{32}PO_4$ uptake was summarized by three main size categories: 0.45–1 μm representing bacteria-size particles, 1–8 μm for smaller nannoplankton, and > 8 μm, which probably included larger nannoplankton and netplankton. The basic seasonal trend in the relative contributions of each size fraction to the total phosphate uptake was similar throughout the Bay (Fig. 4). Larger phytoplankton (> 8 μm) accounted for at least 40% and usually 60–100% of the uptake in May. Uptake by the very large phytoplankton (> 64 μm) made up as much as 50% of the total at times in May. This large size category usually accounted for < 15% of total uptake during the rest of the season. Uptake by particles > 8 μm declined steadily in importance to a minimum in early July of < 15% at all stations. The large phytoplankton (> 8 μm) become much more important during August and September (40–60% of the total phosphate uptake at that time).

Uptake by the nannoplankton (1–8 μm) became increasingly important from late June until early July in the upper bay, making up 45–60% of the total at station B. At station N this fraction was most important in early June (50–60%), declined steadily in importance until the end of August (25–40%), and made up only 15–23% of the total uptake thereafter. Uptake by the 1–8 μm fraction showed no seasonal trends at station HB and GL and varied between 25 and 35% during much of the study. However, the lowest percent uptake (< 20%) by this fraction at HB and GL was in May and September when uptake by algae > 8 μm was highest. Uptake by the 1–8 μm fraction in June at station C was 30–40% of the total, similar to the upper bay. Unlike the rest of the bay, uptake in the 1–8 μm fraction was highest at station C in August (30–40%).

The proportion of the total phosphate uptake by bacteria-size particles (0.45–1 μm) was inversely related to uptake by the larger phytoplankton ($r = -0.86$, $P < 0.01$, no difference with arc sine transformation). Uptake by this smallest size category was low in May, especially at stations HB and C (0–10%). However, the importance of small particles increased during June and peaked in early July when orthophosphate turnover times were most rapid. By early July the 0.45–1 μm fraction accounted for 40–50% of the total phosphate uptake in the upper bay and over 80% in the lower bay. The importance of this size fraction decreased in August and accounted for about 20–30% of total uptake by September.

Total Phosphorus

Only total phosphorus concentrations (total [P]) have been reported here, since estimates of soluble reactive phosphorus are known to overestimate orthophosphate concentrations (Rigler 1966, 1968). Furthermore, the complex and rapid kinetics asso-

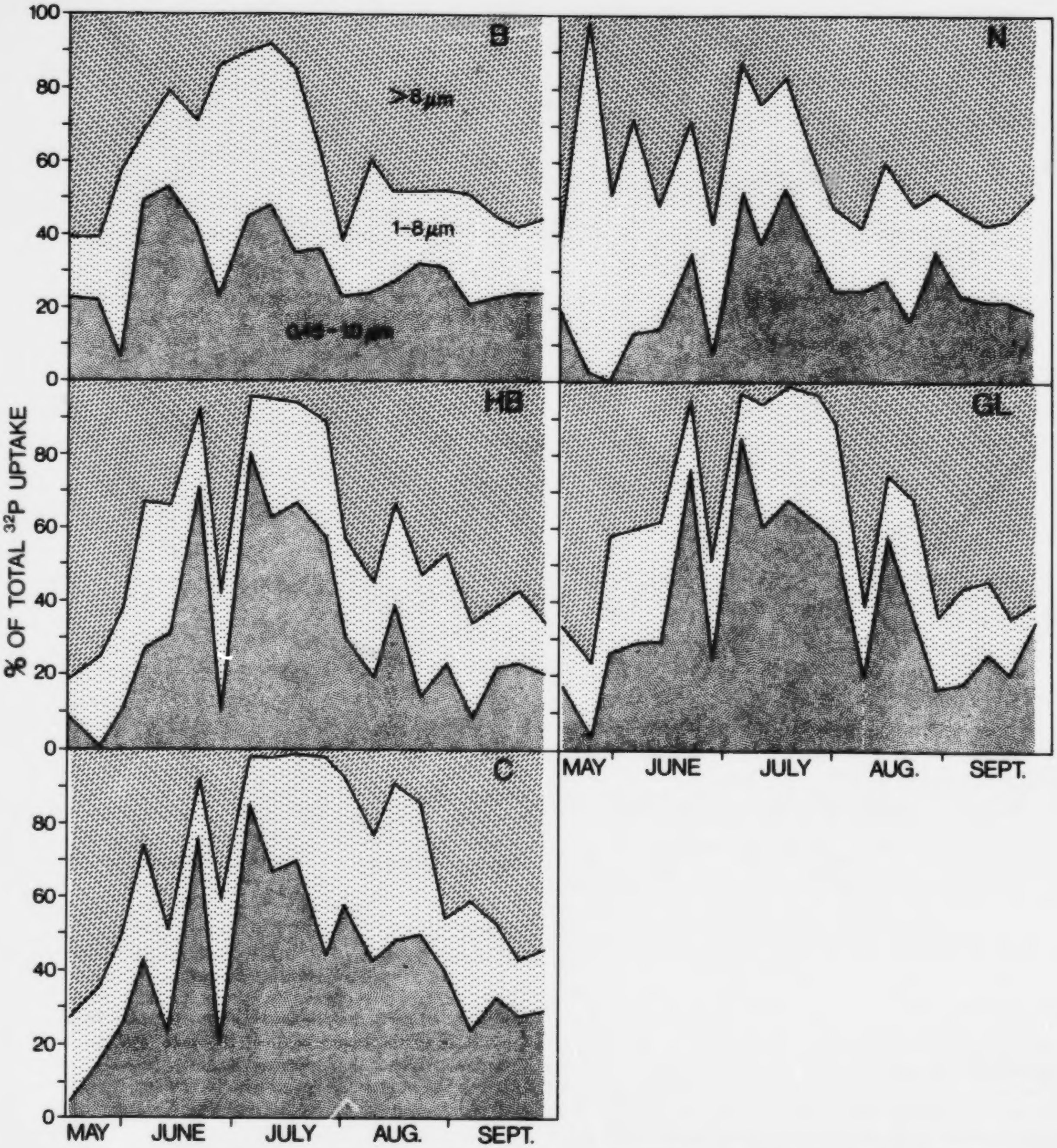

FIG. 4. Percentage of total $^{32}PO_4$ uptake in different size categories at five stations in the Bay of Quinte.

ciated with dissolved fractions of phosphorus (Lean 1973) make it difficult to discuss phosphorus availability using data on static concentrations. A complete presentation of nutrient concentrations and loadings can be found in other papers in this volume (Minns et al. 1986; Robinson 1986).

All stations, except C and LE, showed a marked increase in total [P] from May through September (Fig. 5). In the upper bay, total [P] fluctuated between 20 and 40 mg · m^{-3} in May and June, and increased markedly during July and August (60–70 mg · m^{-3}) and continued to increase in September (80 mg · m^{-3}). Trends were similar in the middle bay but concentrations were lower and tended to lag the upper bay. The largest changes in total [P] occurred in August and September. In the lower bay, total [P] fluctuated between 15 and 20 mg · m^{-3} over the entire season with no distinct pattern.

Chlorophyll *a*

In the upper bay, chlorophyll *a* (Chl *a*) was lowest during May (3–13 mg · m^{-3}) and increased slightly during June (6–27 mg · m^{-3}). Concentrations were generally in the 5–10

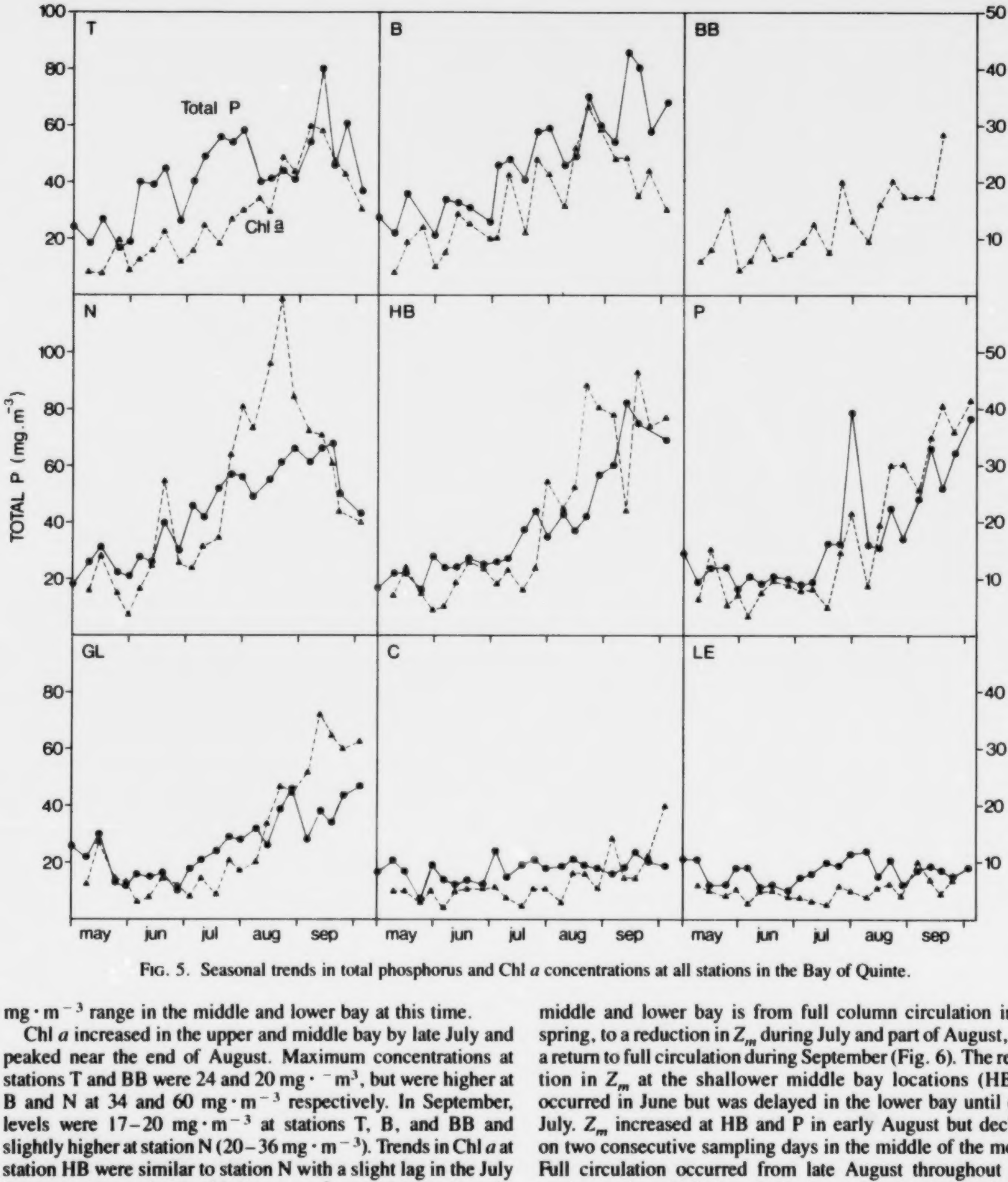

FIG. 5. Seasonal trends in total phosphorus and Chl *a* concentrations at all stations in the Bay of Quinte.

$\text{mg} \cdot \text{m}^{-3}$ range in the middle and lower bay at this time.

Chl *a* increased in the upper and middle bay by late July and peaked near the end of August. Maximum concentrations at stations T and BB were 24 and 20 $\text{mg} \cdot {}^{-}\text{m}^3$, but were higher at B and N at 34 and 60 $\text{mg} \cdot \text{m}^{-3}$ respectively. In September, levels were 17–20 $\text{mg} \cdot \text{m}^{-3}$ at stations T, B, and BB and slightly higher at station N (20–36 $\text{mg} \cdot \text{m}^{-3}$). Trends in Chl *a* at station HB were similar to station N with a slight lag in the July increase. August levels (31.9 $\text{mg} \cdot \text{m}^{-3}$) were higher than the upper bay stations other than N, and maximum levels occurred in late August and September (40–50 $\text{mg} \cdot \text{m}^{-3}$).

At stations P and GL, mean August Chl *a* was lower at 22 and 16 $\text{mg} \cdot \text{m}^{-3}$, respectively, as were maximum levels (35–40 $\text{mg} \cdot \text{m}^{-3}$). Chl *a* at stations C and LE fluctuated from 2 to 8 $\text{mg} \cdot \text{m}^{-3}$ until September when levels reached 10–15 $\text{mg} \cdot \text{m}^{-3}$.

Mixing Depth and Water Column Stability

The basic seasonal trend in vertical mixing depth (Z_m) in the middle and lower bay is from full column circulation in the spring, to a reduction in Z_m during July and part of August, with a return to full circulation during September (Fig. 6). The reduction in Z_m at the shallower middle bay locations (HB, P) occurred in June but was delayed in the lower bay until early July. Z_m increased at HB and P in early August but declined on two consecutive sampling days in the middle of the month. Full circulation occurred from late August throughout September in the middle bay. In the lower bay, Z_m declined markedly from 5 to 18 July but increased gradually throughout August. The mid-August decline in Z_m noted at HB and P was evident only at station GL and on only one sampling date.

Generally, values for N^2 were negatively related to Z_m on the middle and lower bay where thermal stratification occurs (Reynolds et al. 1984; Millard 1986). Values were minimal in May and September when full circulation occurred throughout the middle and lower bay. The maximum and average summer values declined progressing from station HB lakeward. The highest N^2 values (1500 × 10^{-6} to 2500 × $10^{-6} \cdot \text{s}^{-2}$),

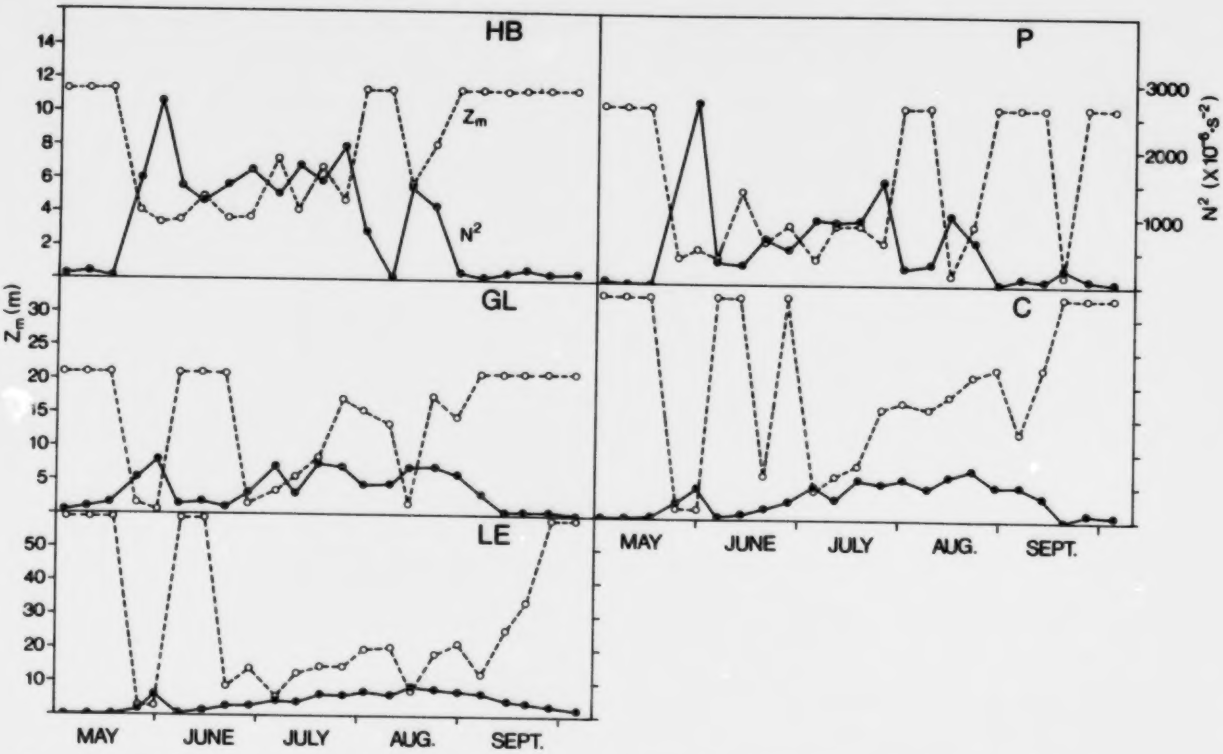

FIG. 6. Seasonal trends in mixing depth (Z_m) and water column stability (N^2) at the middle (HB, P) and lower (GL, C, LE) bay stations.

denoting a very stable water column, were most evident at station HB in June and July. Maximum values at stations GL, C, and LE were only 400×10^{-6} to $700 \times 10^{-6} \cdot s^{-2}$). The mid-August decrease in Z_m at station HB and P was accompanied by an increase in N^2 values. Unlike the middle bay, the August increase in Z_m in the lower bay was associated with maximal N^2 values for each station, indicating a better defined mixing depth.

Discussion

A classification scheme was used to place orthophosphate turnover times into one of three levels of phosphorus demand to quantify the seasonal demand at each station (Fig. 7). In this study, turnover times > 60 min indicated low phosphorus demand, values from 20 to 60 min moderate demand, and turnover times < 20 min high demand. These categories were based on results of several other studies. Lean and Pick (1981) suggested that turnover times of < 20 min mean that phosphate is limiting algal growth. Lean et al. (1983) stated that turnover times of 10–60 min are rapid and mean phosphorus is in great demand. Similarly, Nalewajko and Lee (1981) measured turnover times of 14–40 min in Lake Superior during August and September and concluded that demand was moderate to high. Stations N and HB had high phosphorus demand most frequently, while the upper bay stations T, B, and BB had the fewest occasions with high phosphorus demand. Station BB showed the lowest phosphorus demand of all stations. The shortest turnover time at station BB was 25.6 min and turnover times fell in the moderate demand category on only three other occasions at this location. The lower bay stations also had turnover times that frequently fell in the lower demand category.

The high phosphorus demand from station N lakeward to LE in late June and early July indicated that available phosphorus supplies were depleted. This was also the only period in the upper bay when demand was moderate to high. Available phosphorus supplies were likely depleted by the annual spring diatom growth that occurs throughout the bay (Nicholls et al. 1986). At this time, *Stephanodiscus astraea* (Ehr.) Grun., and to a lesser extent *Synedra acus* Kutz, *Tabellaria fenestrata* (Lyngbye) Kütz, *Fragillaria crotonesis* Kitt., and *Melosira* spp., dominate the phytoplankton community. This explains the importance of the larger size fractions in phosphorus uptake during May. Other evidence points to phosphorus limitation of algal growth at this time of the season. Nicholls et al. (1986) showed that both the length of the spring *Stephanodiscus* spp. growth period and the decline in silica levels were positively related to phosphorus concentrations. In addition rapid phosphate turnover times, the importance of bacteria-size particles in phosphorus uptake, type 2 uptake curves and the relatively low Chl *a* levels are other factors that suggest phosphorus supply was critical in late June. Bacteria and small algae often dominate phosphorus uptake when turnover times are rapid (Rigler 1956). When bacteria dominate phosphorus uptake, turnover times do not directly reflect phosphorus demand by algae. However, since uptake by bacteria is easily saturated with small additions of phosphorus, bacteria-dominated uptake indicates that the entire plankton, including larger algae, is phosphorus deficient (Lean 1984). Short turnover times indicate high phosphorus demand relative to supply. When algal biomass is low and turnover times are rapid, further increases in standing crop may be prevented by phosphorus limitations on algal growth (Lean and Pick 1981; Lean et al. 1983).

Throughout the bay there was an increase in phosphate turnover times, total algal biomass, and a dominance of larger size

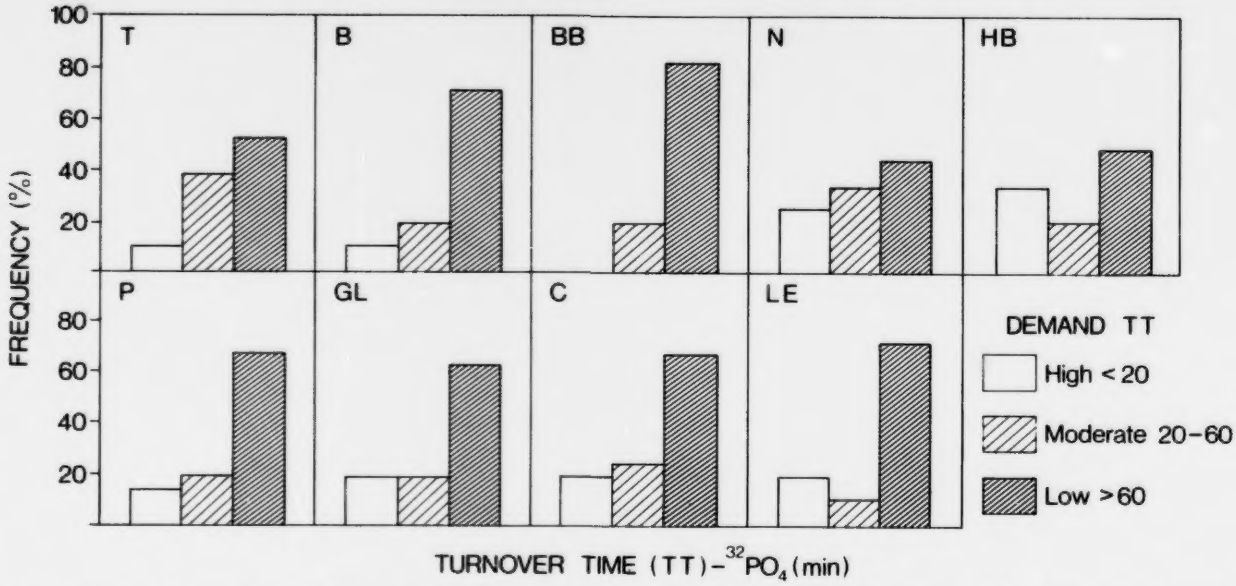

FIG. 7. Freqency histogram showing distribution of $^{32}PO_4$ turnover times in different phosphorus demand categories at each of the nine sampling locations.

fractions in phosphate uptake by August, indicating an increase in available phosphorus. An increase in phosphorus supply can cause the transition from rapid phosphorus kinetics dominated by bacteria and small algae, that occurred in early July, to slower turnover times when larger algae take up much of the phosphate as in August (Lean and White 1983).

The increase in total [P] in the upper bay during July and August (50–56 $mg \cdot m^{-3}$) to double June values (Robinson 1986) shows that phosphorus supply increased. Part of this increase in concentrations occurred annually because of low summer flow (Johnson and Owen 1971). However, in 1978 part of the summer increase in total [P] must have been due to sediment regeneration of phosphorus (Minns et al. 1986).

Higher phosphorus demand might have been expected in the lower bay because of lower total [P] compared with upper bay and therefore potentially less available phosphorus. Lower total [P] in the lower bay was caused by dilution of bay water by intrusions of Lake Ontario water (Minns et al. 1986). Although these intrusions can occur as far up the bay as station HB, their effect is largely confined to stations GL, C, and LE (Freeman and Prinsenberg 1986). In constrast, lower algal growth rates because of a lag in warming and effects of deep mixing on net photosynthesis (Millard 1986) may have lowered phosphorus demand in the lower bay at times. Deep mixing in western Lake Erie (Lean and Nalewajko 1979) and Lake Superior (Nalewajko and Lee 1981) has been given as an explanation for low phosphorus demand.

The reduction in Z_m and increased stability of the water column in early July put additional stress on phosphorus supplies in the middle and lower bay. This may partially explain the more rapid turnover times compared with the upper bay during this period. Shorter mixed depths reduced the size of the available phosphorus pool and shut off supplies of phosphorus from deep water or sediment regeneration. A decrease in Z_m probably caused the rapid turnover times at station HB and N in August. Shorter Z_m and higher N^2 occurred to a lesser extent at stations P and GL in August with less of an effect on phosphate turnover times (20–30 min). Timing of stratification is also thought to be important in determining seasonal patterns of phosphorus limitation in Lake Erie (Lean et al. 1983).

Seston at stations N and HB had the highest phosphorus demand. In the middle bay this was due in part to earlier, stronger, and more persistent thermal stratification than in the lower bay. At station N, total [P] and point-source phosphorus loadings from Napanee were equal to those at station B farther up the bay. However, the difference in phosphorus demand indicates that available phosphorus was in shorter supply. The exposed location of stations B and BB may have increased the frequency of mobilization of phosphorus from sediments during windy weather. An added supply of available phosphorus such as this may account for the consistently low demand at these stations. The location of station N with respect to the Napanee River and the Napanee sewage treatment plant may also have been an important factor in reducing the effectiveness of this point source of phosphorus. Part of the available phosphorus from the Napanee sewage plant was probably taken up by dense algal and macrophyte growth along the Napanee River after the sewage outfall. In addition, the location of station N placed it more directly under the influence of higher flow from the upper bay than the low summer flow from the river. The high algal biomass at station N was a stress on available phosphorus supply and caused the rapid turnover times. Algal standing crops from station N through Long Reach to HB were dependent on rapid recycling of phosphorus and were probably more representative of the high phosphorus supply farther up the bay. The distance from effective point sources of available phosphorus was probably of increasing importance progressing from the upper to middle bay regions.

Rapid phosphate turnover times in the middle and lower bay indicated that phosphorus supply was immediately limiting to algal growth at times in the summer. This was not as apparent in the upper bay although turnover times did decrease in July and early August. In spite of this lower phosphorus demand and a late summer increase in phosphorus supply from sediment regeneration, seasonal primary production was lower in 1978 in the upper bay than in all years prior to phosphorus control

(Millard and Johnson 1986). It appears that over a time frame of weeks to months, turnover times may not have to become extremely rapid for changes in phosphorus supply to reduce algal standing crop and production. Further reductions in phosphate turnover times sustained over a longer period would undoubtedly be reflected in even lower primary production. This may not be achieved until surface sediments in the upper bay export phosphorus and come into equilibrium with external phosphorus loadings (Minns et al. 1986).

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References

Brown, L. C. 1971. Determination of phosphorus-32 and -33 in aqueous solution. Anal. Chem. 43: 1326–1328.

Burnison, B. K. 1975. Microbial ATP studies. Verh. Int. Ver. Limnol. 19: 286–290.

Chow-Fraser, P., and H. C. Duthie. 1983. Assessment of phosphorus limitation in an oligotrophyic lake using radiophosphorus uptake kinetics. Can. J. Fish. Aquat. Sci. 40: 817–821.

Environment Canada. 1979. Analytical methods manual. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

Freeman, N. G., and S. J. Prinsenberg. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G., and D. A. Hurley. 1986. Overview of Project Quinte — 1972–82, p. 1–6. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario, Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G., and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

Lean, D. R. S. 1973. Phosphorus movement between biologically important forms in lake water. J. Fish. Res. Board Can. 30: 1525–1536.

1984. Metabolic indicators for phosphorus limitation. Verh. Int. Ver. Limnol. 22: 211–218.

Lean, D. R. S., A. P. Abbott, M. N. Charlton, and S. S. Rao. 1983. Seasonal phosphate demand for Lake Erie phytoplankton. J. Great Lakes Res. 9 (1): 83–91.

Lean, D. R. S., and B. K. Burnison. 1979. An evaluation of errors in the ^{14}C method of primary production measurements. Limnol. Oceanogr. 24: 917–928.

Lean, D. R. S., and C. Nalewajko. 1979. Phosphorus turnover time and phosphorus demand in large and small lakes. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13: 120–132.

Lean, D. R. S., and F. R. Pick. 1981. Photosynthetic response of lake plankton to nutrient enrichment: a test for nutrient limitation. Limnol. Oceanogr. 26: 1001–1019.

Lean, D. R. S., and F. H. Rigler. 1974. A test of the hypothesis that abiotic phosphate complexing influences phosphorus kinetics in lakewater. Limnol. Oceanogr. 19: 784–788.

Lean, D. R. S., and E. White. 1983. Chemical and radiotracer measurements of phosphorus uptake by lake plankton. Can. J. Fish. Aquat. Sci. 40: 147–155.

Levine, S. N., and D. W. Schindler. 1980. Radiochemical analysis of orthophosphate concentrations and seasonal changes in the flux of orthophosphate to seston in two Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 479–487.

Millard, E. S. 1986. Effect of light climate, photosynthetic capacity, and respiration on gross integral primary production and net primary production potential in the Bay of Quinte, Lake Ontario, p. 128–138. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Millard, E. S., and M. G. Johnson 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nalewajko, C., and K. Lee. 1981. Phosphorus kinetics in Lake Superior: light intensity and phosphate uptake in algae. Can. J. Fish. Aquat. Sci. 38: 224–232.

Nicholls, K. H., L. Heintsch, E. Carney, J. L. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Peters, R. H. 1974. Carrier contamination of "SORIN" radiophosphate. Mem. Ist. Ital. Idrobiol. 31: 61–68.

1975. Orthophosphate turnover in Central European lakes. Mem. Ist Ital. Idrobiol. 32: 297–311.

Phillips, O. M. 1966. The dynamics of the upper ocean. Cambridge University Press, Cambridge.

Reynolds, C. S., S. W., Wiseman, and M. S. O. Clarke. 1984. Growth- and loss-rate responses of phytoplankton to intermittent artificial mixing and their potential application to the control of planktonic algal biomass. J. Appl. Ecol. 21: 11–39.

Riggs, D. S. 1967. The mathematical approach to physiological problems. MIT Press, Cambridge, MA 445 p.

Rigler, F. H. 1956. A tracer study of the phosphorus cycle in lake water. Ecology 37: 550–562.

1964. The phosphorus fractions and the turnover time of inorganic phosphorus in different types of lakes. Limnol. Oceanogr. 9: 511–518.

1966. Radiobiological analysis of inorganic phosphorus in lake water. Verh. Int. Ver. Limnol. 16: 465–470.

1968. Further observations inconsistent with the hypothesis that the molybdenum-blue method measures orthophosphate in the lake water. Limnol. Oceanogr. 13: 7–13.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

White, E., G. Payne, S. Pickmere, and F. R. Pick. 1982. Factors influencing orthophosphate turnover times: a comparison of Canadian and New Zealand lakes. Can. J. Fish. Aquat. Sci. 39: 469–474.

Effect of Decreased Phosphorus Loading on Primary Production, Chlorophyll *a*, and Light Extinction in the Bay of Quinte, Lake Ontario, 1972–82

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A study was carried out in the Bay of Quinte, Lake Ontario from 1972 to 1982 to determine the effectiveness of phosphorus (P) controls (1978–82) at lowering chlorophyll *a* (Chl *a*) concentrations, primary production rates (A_{max}), and light extinction (ε_{PAR}). Prior to P controls, conditions in the upper bay placed it amongst some of the most eutrophic temperate-climate lakes in the world. Rapid increases to high peak values in Chl *a* (60–100 mg · m^{-3}), A_{max} (400–500 mg C · m^{-3} · h^{-1}), and ε_{PAR} (2.75–3.75 · m^{-1}) occurred each summer prior to P control. Following P controls, summer means and maxima for these parameters have declined substantially. Total gross primary production (May–September) has declined 37–46% in the upper bay and 26–28% in the middle and lower bay. The gradient from upper to lower bay in parameters such as Chl *a*, A_{max}, and ε_{PAR}, directly influenced by algal density, was less pronounced after P control. Self-shading properties of the phytoplankton community reduced the differences between regions of the bay in integral primary production (ΣA, mg C · m^{-2} · h^{-1}) but this was even more evident with P control. River flow and point-source P loadings explained much of the variance in P concentrations and thus productivity in the upper bay.

De 1972 à 1982, on a effectué une étude dans la baie de Quinte (lac Ontario) afin de déterminer l'efficacité des mesures de réduction du phosphore (P) (de 1978 à 1982) pour diminuer les concentrations de chlorophylle *a* (Chl *a*), les taux de production primaire (A_{max}), et le degré d'extinction de la lumière (ε_{par}). Avant qu'on applique des mesures de réduction de P, les conditions dans la partie supérieure de la baie plaçaient celle-ci dans la même catégorie que certains des lacs plus eutrophes des régions tempérées du globe. Chaque été, avant qu'on limite les apports de P, il y a eu une augmentation rapide jusqu'à des valeurs maximales élevées de Chl *a* (60–100 mg · m^{-3}), d'A_{max} (400–500 mg · m^{-3} · h^{-1} de C) et de ε_{par} (2,75–3,75 · m^{-1}). Depuis les mesures de réduction de P, les moyennes et les maxima enregistrés l'été pour ces paramètres ont diminué sensiblement. La production primaire brute totale (de mai à septembre) a diminué de 37 à 46 % dans la partie supérieure de la baie et de 26 à 28 % dans les parties médiane et inférieure. Le taux de variation des paramètres comme la Chl *a*, l'A_{max} et le ε_{par}, qui sont influencés directement par la densité des algues, a été moins prononcé entre les parties supérieure et inférieure de la baie après la réduction du P. La capacité qu'a la communauté phytoplanctonique de se protéger elle-même du soleil a atténué les différences observées entre les diverses régions de la baie dans la production primaire intégrale (ΣA, mg · m^{-2} · h^{-1} de C), mais cela a été encore plus évident suite à la réduction du P. Le débit des rivières et les charges ponctuelles de P expliquaient une bonne partie de la variance des concentrations de P et, par conséquent, de la productivité dans la partie supérieure de la baie.

Introduction

This paper describes seasonal trends as well as differences between years and locations for primary production, chlorophyll *a* (Chl *a*) and vertical light extinction in the Bay of Quinte, Lake Ontario, from 1972 to 1982. This study was done within the framework of Project Quinte, a multi-agency project designed to look at the response of an eutrophic ecosystem to reductions in phosphorus (P) loading. The pre-P control period was 1972–77 with P control starting in 1978. Much of the data analysis and explanation in this paper deals with monthly and seasonal means. This is a lengthy time frame compared with the short time required by phytoplankton to adapt to many environmental influences (Harris 1980). However, another paper in this issue deals with seasonal interrelationships of determinants of primary production in greater detail (Millard 1986b).

One of the primary objectives of Project Quinte was to determine to what extent the proposed reductions in P loadings (Johnson and Hurley 1986) would result in lower algal standing crops. At the start of Project Quinte it was clearly established that the key to controlling eutrophication was by reducing P loading (Vollenweider 1968; Schindler 1971; Likens 1972). P supply is the key because it determines the carrying capacity or maximum attainable algal biomass in most lakes (Schindler et

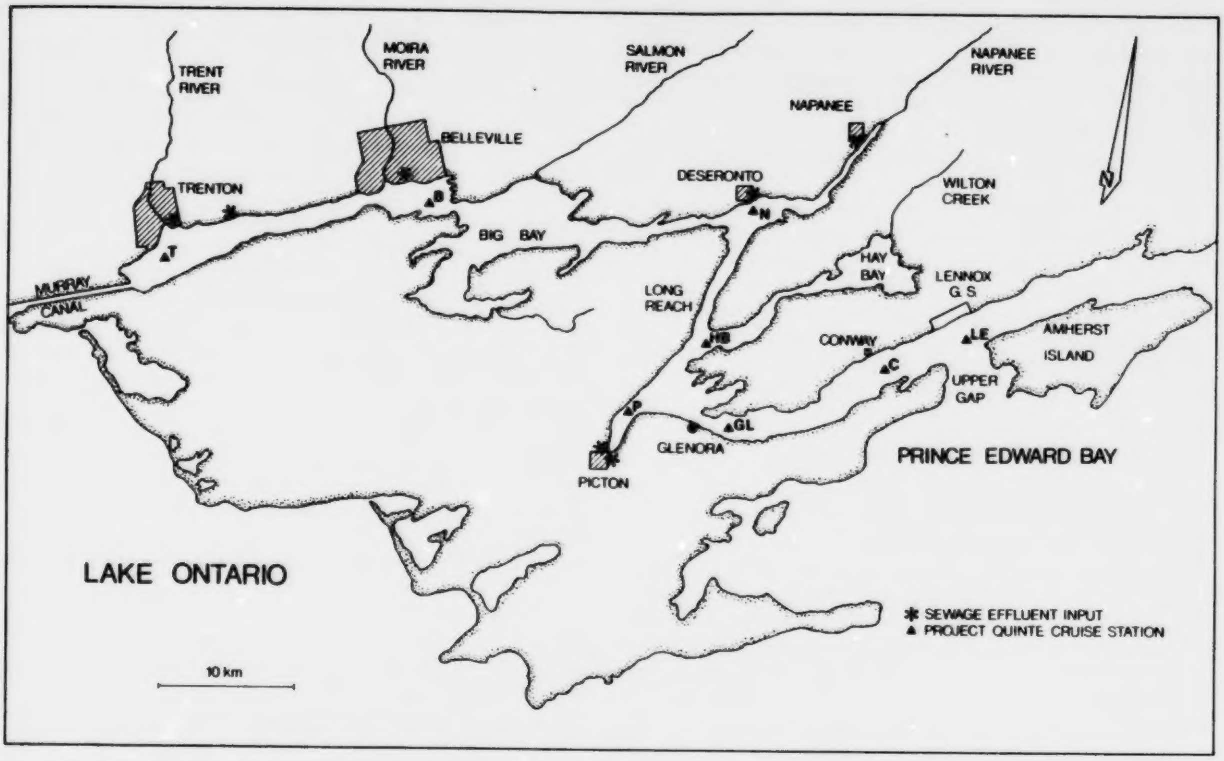

FIG. 1. Bay of Quinte and sampling locations; upper bay stations are T, B, and N, middle bay stations are HB and P, and lower bay stations are GL, C, and LE.

al. 1973). Improved water quality due to reduction in P supply has since been documented for a number of lakes. The best known examples are Lake Washington (Edmondson 1977), Gravenhurst Bay, Lake Muskoka (Dillon et al. 1978), several Swedish lakes (Forsberg 1979) and the lower Madison lakes (Sonzogni et al. 1974).

In the upper Bay of Quinte, high point-source P loadings (PSL) and reduced summer flushing rates (Johnson and Owen 1971; Minns et al. 1986) created a eutrophic, polluted environment (Rodhe 1969). The effectiveness of P controls in the shallow, well-mixed, upper bay where sediments were highly P enriched was uncertain (Johnson and Hurley 1986). There are numerous cases where recovery due to P control has been delayed because of sediment regeneration of P such as Lake Norrviken, Sweden (Ahlgren 1977), Shagawa Lake, Minnesota (Larsen et al. 1979), and Lakes Glaningen and Uttran, Sweden (Forsberg 1979). This study provided a chance to assess the importance of changes in P supply relative to other factors such as temperature, light, and mixing. Furthermore, the P control program for the Great Lakes benefited from a study of the effectiveness of such a program in a system where many unmanageable factors such as depth, temperature, low summer flushing, and P-enriched sediments favoured high primary production.

Materials and Methods

Sampling

Sampling cruises were made weekly from May until the end of September at up to eight stations from 1972 to 1982 (Fig. 1). Stations were always visited in the same order to keep time of day constant. Stations T, B, and N were sampled on the first day, C, GL, HB, and P on the second, and LE on the third day in the years it was sampled (1975–78). Stations B, N, HB, GL, and C were sampled throughout the season in all years. Stations T and P were sampled weekly from 1972 to 1978. In 1979 and 1980, T was sampled weekly in June and August only. Stations T, B, and N were considered to be upper bay, HB and P middle bay, and GL, C, and LE lower bay.

Light Extinction

Light measurements were made with a submarine photometer equipped with a selenium photocell, a diffusing filter, but no colour filters (Model 268WA310, Kahl Scientific Inst. Co., San Diego, CA). Light profiles were made through the euphotic zone every 0.25–0.50 m in the upper bay and every 0.50–1.00 m in the lower bay. A deck-cell was used to check for constant incident light during each profile. Vertical extinction coefficients for visible light were calculated by the method of Vollenweider (1974). Euphotic zone depths (Z_{eu} = 1% penetration) can be calculated as $Z_{eu} = \ln 100/\varepsilon_{PAR}$.

Chlorophyll *a*

Composite samples were collected by lowering and raising bottles at a constant speed through an approximation of the euphotic zone (2 × Secchi disc visibility). Samples were filtered through 1.2-µm membrane filters (Millipore Co.), frozen, and later analyzed at the Ministry of the Environment Laboratory, Rexdale, Ont., using methods outlined in their manual

(Ministry of the Environment 1981). From 1977 to 1982, replicate samples were filtered through GF/C glass-fibre filters (Whatman Co.), frozen, and analyzed later at the Canada Centre for Inland Waters (Environment Canada 1979). This latter method involves grinding in 90% acetone and yields higher chlorophyll values than the membrane method (Long and Cooke 1972).

A regression between values obtained with the glass-fibre filter method and the membrane filter method showed that the latter method underestimated Chl *a* concentrations ($Y = 0.12 + 1.30X$, $r = 0.92$, $n = 560$). In fact, underestimates were often more serious at higher concentrations than predicted from the regression equation. However, the high correlation suggests that although peak concentrations were underestimated, seasonal trends were adequately described in earlier years.

Primary Production

Primary production rates were measured using the light–dark bottle oxygen method (Vollenweider 1974). Bottles were placed horizontally in a shipboard incubator exposed to the sun. The incubator was a shallow (12 cm) wood box divided into six chambers with sheets of translucent plastic mounted in removable frames over each compartment. One chamber was left uncovered to represent surface light conditions. A gradient of percent transmission was made by varying the number of sheets over each compartment. Green cellophane was placed between the sheets in the chamber with the lowest transmission (3%) to get a greater reduction in transmission and simulate the usual dominance of green light at greater depths (Millard 1986b). In 1981 and 1982, a neutral-density plastic film was used instead of green cellophane to get the proper gradient of transmission in the last two chambers (7 and 3%). Each season, percent transmission of the screens for each chamber was measured with the photometer. Percent transmissions for the six chambers over the study period were approximately 100, 65–67, 45–55, 20–26, 7–16, and 3%. Surface water was pumped continuously through the box to maintain a constant temperature.

Water samples were collected from depths corresponding to the percent transmission of each chamber found by interpolation on the percent transmission versus depth plot. N_2 was bubbled through the water before filling the bottles to reduce oxygen concentration to 40–50% of saturation. This reduced the loss of oxygen in light bottles due to supersaturation during periods of intense photosynthesis. Two light and two dark bottles (300 mL BOD) were filled and incubated from each depth. A fifth bottle was also filled and the initial oxygen concentration measured. Bottles were incubated 3–4 h in the upper bay and 4–5 h in the lower bay. Oxygen concentrations at the end of incubations were measured using a YSI (Yellow Springs Instrument Co.) model 54 oxygen meter and probe from 1972 to 1978. From 1979 to 1982 an Orbisphere meter (Orbisphere Laboratories, Switzerland) was used. Rates of gross photosynthesis ($\mathrm{mg\,O_2 \cdot m^{-3} \cdot h^{-1}}$) were calculated and converted to carbon using a photosynthetic quotient of 1.25 (Ryther 1956). These rates were plotted at depths determined by the extinction coefficient and chamber transmission and integrated to give area-based rates ($\mathrm{mg\,C \cdot m^{-2} \cdot h^{-1}}$).

Calculation of Daily Integral Primary Production

Short-term measurements of integral production made in the incubator were expanded to daily rates ($\mathrm{mg\,C \cdot m^{-2} \cdot d^{-1}}$) using the semi-empirical model of Talling (1957):

$$\Sigma\Sigma A = \frac{A_{\max}}{a \cdot \varepsilon_{\min}} \cdot 0.9\Delta t\,(\ln \bar{I}_o - \ln 0.5 I_K).$$

The light-saturated rate of gross primary production, $A_{\max}$ ($\mathrm{mg\,C \cdot m^{-3} \cdot h^{-1}}$), was determined from the depth profiles. The constant *a* corrects for the overestimate of penetration of total visible light when the extinction coefficient for the most penetrating part of the visible spectrum ($\varepsilon_{\min}$) is used. In this study, values for ε_{PAR} were obtained with an unfiltered photocell with a fairly equal response to light energy throughout most of the visible range. These estimates of ε_{PAR} agreed closely with estimates of ε_{PAR} made with a quantaspectrometer (Incentive Research and Development, Sweden) (Millard 1986b). As a result, ε_{PAR} was used in the model instead of $a \cdot \varepsilon_{\min}$. Data for day length ($\Delta t$) were obtained from meteorological tables (Smithsonian Institution 1951). The value 0.9 is an empirical factor used to correct for the effectiveness of day length on dull days and the slight overestimates that arise from using the mean incident light intensity during the day ($\bar{I}'_o$) (Talling 1957). The parameter I_K defines the irradiance level at which light saturation of photosynthesis starts. Graphically, its value can be determined from photosynthetic rate versus irradiance plots as the irradiance where extrapolation of the linear portion of the curve intersects the asymptote or light-saturated rate. It was difficult to obtain consistently reliable I_K values using this method with our data because most profiles had only one or two points in the linear part of the curve. As a result, constant values of 3.0 $\mathrm{g\,cal \cdot cm^{-2} \cdot h^{-1}}$ for the upper bay and 2.5 $\mathrm{g\,cal \cdot cm^{-2} \cdot h^{-1}}$ for the lower bay of photosynthetically available radiation (PAR) were used in the model. In this and other studies, the light-independent ratio $A_{\max}/\varepsilon_{PAR}$ explains most of the variation in integral production (Bindloss 1974; Jewson 1976; Jones 1977; Harris et al. 1980), suggesting that errors arising from using a constant I_K value may not be that important over the course of the season if the estimate is reasonable (see Millard 1986b for further discussion). Irradiance was measured continuously with a Kipp and Zonen pyranometer located in the vicinity of the Ministry of Natural Resources Fisheries Station, Picton, Ont. Maintenance and calibration of the sensor and recording instruments were performed by the Technical Operations Section, Canada Centre for Inland Waters. Corrections of 46 and 10% were applied to total measured radiation to correct for proportions of PAR and reflection losses, respectively (Vollenweider 1974).

Symbols and Abbreviations

Chl *a*	Chlorophyll *a* ($\mathrm{mg \cdot m^{-3}}$)
ε_{PAR}	Vertical extinction coefficient for visible light (400–700 nm) ($\mathrm{m^{-1}}$)
$A_{\max}$	Light-saturated rate of gross primary production per unit volume of water ($\mathrm{mg\,C \cdot m^{-3} \cdot h^{-1}}$)
ΣA	Hourly rate of gross primary production per unit area ($\mathrm{mg\,C \cdot m^{-2} \cdot h^{-1}}$)
$\Sigma\Sigma A$	Daily rate of gross primary production per unit area ($\mathrm{mg\,C \cdot m^{-2} \cdot d^{-1}}$)
PAR	Photosynthetically available radiation (400–700 nm)
I'_o	Mean irradiance (PAR) just below the water surface during the incubation time ($\mathrm{g\,cal \cdot cm^{-2} \cdot h^{-1}}$)
$\bar{I}_o$	Mean irradiance (PAR) just below the water surface during the day ($\mathrm{g\,cal \cdot cm^{-2} \cdot h^{-1}}$)
I_K	Irradiance (PAR) indicating the onset of light saturation of primary production ($\mathrm{g\,cal \cdot cm^{-2} \cdot h^{-1}}$)
Δt	Day length (h)
Z_{eu}	Depth of euphotic zone (m), 1% penetration of I'_o

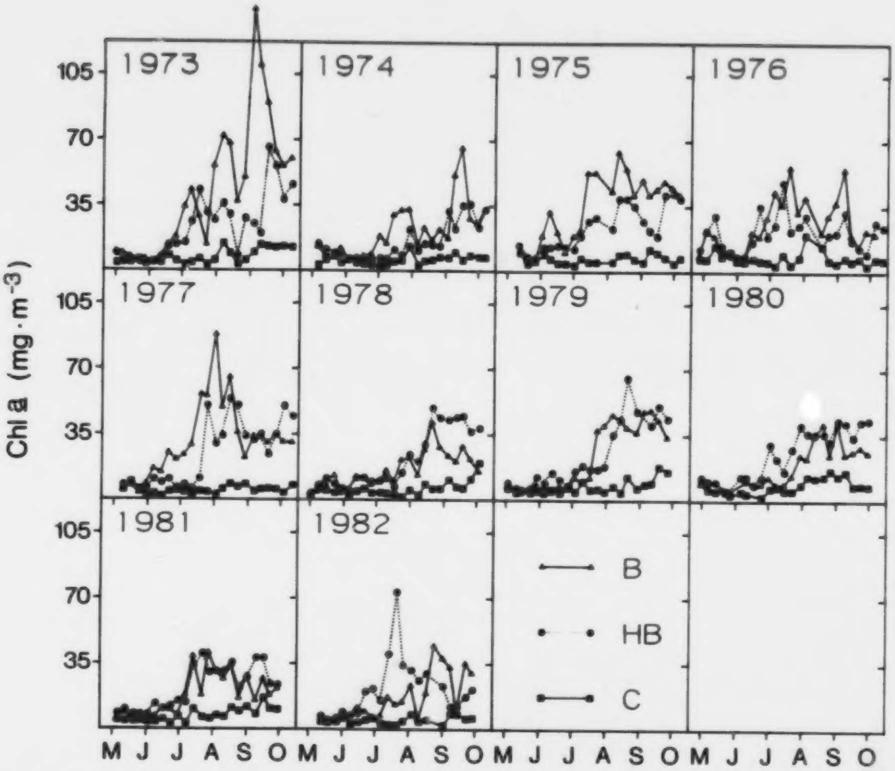

FIG. 2. Seasonal trends in Chl *a* at stations representing the upper (B), middle (HB), and lower (C) Bay of Quinte from 1973 to 1982. Values are uncorrected for phaeopigments from 1973 to 1976 and corrected from 1977 to 1982.

Results

Seasonal Variation

Chlorophyll a

Seasonal trends in Chl *a* for stations B, HB, and C have been presented as representative of the upper, middle, and lower regions of the bay (Fig. 2).

Chl *a* in the upper bay during June was reduced following P control. Average concentrations declined from about 20 mg · m^{-3} (1975–77) to less than 10 mg · m^{-3} in all postcontrol years. Concentrations increased during July and August, particularly in precontrol years when maximum values were usually greater than 60 mg · m^{-3} and as high as 140 mg · m^{-3} in 1973. September levels were often as high as July and August levels. September monthly mean Chl *a* declined from 28–101 mg · m^{-3} ($\bar{x}$ = 49.0) in precontrol years to a range of 22–43 mg · m^{-3} ($\bar{x}$ = 29.5) in postcontrol years. There was a tendency for maximum Chl *a* levels to occur later after P control. Maxima occurred in late August or early September in four of the postcontrol years. In three of the precontrol years, maxima were reached between late July and early August.

Spring Chl *a* levels in the middle bay were similar to the upper bay. June concentrations did not show the same reduction in postcontrol years that occurred in the upper bay. Concentrations increased in July, with highest monthly means and maxima usually occurring in August and September, although this trend was variable among all years. Chl *a* was not reduced during these months in the postcontrol period in the middle bay.

Chl *a* was always lowest at station C where monthly means in May, June, and July were consistently under 6.0 mg · m^{-3}. Higher values occurred in August and September, but maxima were rarely greater than 15 mg · m^{-3}. Mean concentrations for these months were less, from 6 to 13 mg · m^{-3}. There was considerable overlap between pre- and postcontrol concentrations during the entire season in the lower bay.

A_{max}

The lowest values for A_{max} in the upper bay occurred in May and June (Fig. 3). Rates were usually 50–150 mg C · m^{-3} · h^{-1} in precontrol years and consistently less than 100 mg C · m^{-3} · h^{-1} during these months in postcontrol years. The seasonal trend in A_{max} was usually dominated by dramatic increases during the summer in the upper bay. This was particularly evident in 1973, 1975, and 1977, when A_{max} exceeded 400 mg C · m^{-3} · h^{-1} and was over 500 mg C · m^{-3} · h^{-1} at station N in 1975. Almost every postcontrol monthly mean for A_{max} was lower than in precontrol years in the upper bay. Furthermore, reductions in summer means and maxima for A_{max}, ε_{PAR}, and Chl *a* were most evident in the upper bay (Table 1). There was also a tendency for peak values of A_{max} to occur in August rather than July during postcontrol years, and in 1981 there was no distinct peak in A_{max} at all.

The seasonal trend was similar for A_{max} at station HB, although summer rates were usually less than in the upper bay and changes often lagged the upper bay by 1–2 wk. Summer values of A_{max} in the precontrol period, particularly the high-production years in 1973, 1975, and 1977, often exceeded 200 mg C · m^{-3} · h^{-1}, with extremes of over 300 mg C · m^{-3} · h^{-1}. The distinction between the upper and middle bay in summer levels of A_{max} was less evident in postcontrol

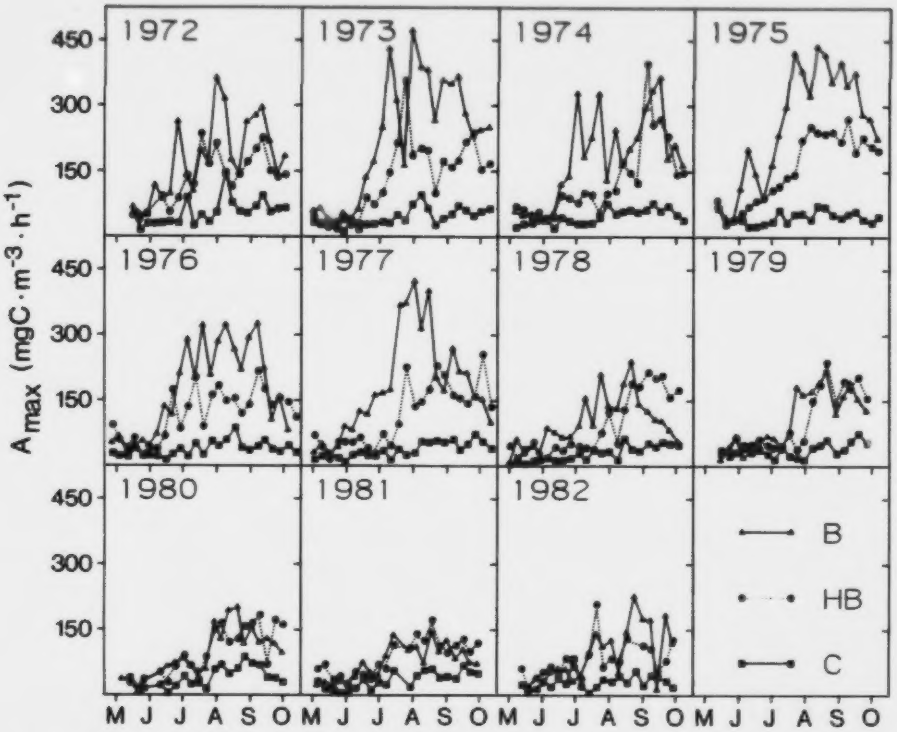

FIG. 3. Seasonal trends in A_{max}, the light-saturated rate of primary production, at stations representing the upper (B), middle (HB), and lower (C) Bay of Quinte from 1972 to 1982.

TABLE 1. Maximum values in each year for A_{max} (mg C · m^{-3} · h^{-1}), ε_{PAR} (m^{-1}), and Chl *a* (mg · m^{-3}) at five stations in the Bay of Quinte.

	B			N			HB			GL			C		
Year	A_{max}	ε_{PAR}	Chl *a*	A_{max}	ε_{PAR}	Chl *a*	A_{max}	ε_{PAR}	Chl *a*	A_{max}	ε_{PAR}	Chl *a*	A_{max}	ε_{PAR}	Chl *a*
1972	363	2.56	—	425	2.42	—	235	2.00	—	153	1.18	—	147	1.10	—
1973	472	2.71	140	533	2.71	96	358	2.00	66	206	1.25	24	96	0.89	15
1974	365	3.18	66	505	2.88	61	397	2.63	36	152	1.40	28	76	1.03	13
1975	437	3.07	64	519	3.18	73	270	2.05	41	195	1.12	22	71	0.99	12
1976	326	3.18	56	288	3.07	65	217	2.09	48	163	1.25	28	87	0.94	20
1977	432	3.07	88	450	3.76	107	256	2.22	54	157	1.15	27	73	0.76	10
1978	239	2.19	41	263	2.49	71	215	1.84	49	146	1.24	31	63	0.96	20
1979	216	2.97	48	257	2.79	70	238	2.71	66	125	1.35	33	74	0.94	18
1980	201	2.25	41	185	2.30	49	184	1.81	43	126	1.42	30	88	0.83	17
1981	146	1.92	41	226	2.34	64	173	2.30	40	106	1.21	28	68	0.87	17
1982	227	2.30	45	333	3.29	104	209	2.56	73	63	1.10	15	84	0.75	8

years. There was also a tendency for a later rise to peak values of A_{max} in postcontrol years, as in the upper bay. The level of A_{max} remained high during September in the middle bay; however, rates were lower in postcontrol compared with precontrol years.

The lowest levels of A_{max} at any time of the season occurred at station C. However, differences with other parts of the bay were least during May and June when rates were typically 20–50 mg C · m^{-3} · h^{-1}. In June, A_{max} showed less consistent reduction in the postcontrol versus precontrol periods at middle and lower bay stations than in the upper bay. The lower bay lacked the sharp increase in A_{max} during the summer that was typical of the rest of the bay. Maximum values in the lower bay were typically 80–100 mg C · m^{-3} · h^{-1} and occurred in August and September. There was no consistent reduction in summer means or extremes in the postcontrol period.

Light extinction, ε_{PAR}

Values for ε_{PAR} were lowest in the upper bay during May (0.70–0.80 · m^{-1}) but reached 1.50–2.00 · m^{-1} in June (Fig. 4). However, in the postcontrol period, ε_{PAR} did not exceed 1.50 · m^{-1} in June, with little change in May values from previous years. Similar to A_{max}, ε_{PAR} increased markedly during the summer, particularly in precontrol years when values were frequently over 2.0 · m^{-1} (Z_{eu} = 2.3 m), with extremes exceeding 3.0 · m^{-1} (Z_{eu} = 1.5 m). Summer means and maxima for ε_{PAR} have declined in postcontrol years. For example, July monthly means have declined from close to or over 2.0 · m^{-1} in the precontrol years to 1.34–1.58 · m^{-1} in the postcontrol period.

Seasonal trends in ε_{PAR} were similar in the middle bay. Values were slightly less during May and June compared with

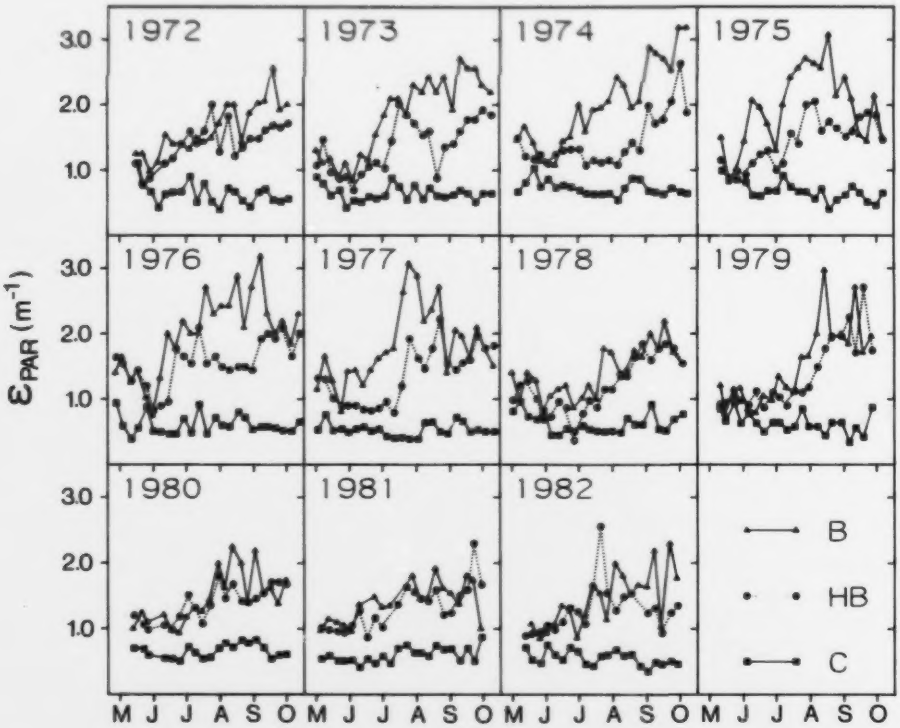

FIG. 4. Seasonal trends in ε_{PAR}, the vertical extinction coefficient for visible light, at stations representing the upper (B), middle (HB), and lower (C) Bay of Quinte from 1972 to 1982.

the upper bay and declined less during the postcontrol compared with the precontrol period than at station B. Values for ε_{PAR} increased in July to about $1.00-1.80 \cdot m^{-1}$ and were highest in most years during August and September at $1.50-2.00 \cdot m^{-1}$ (Z_{eu} = 3.1 − 2.3 m), with extremes of over $2.00 \cdot m^{-1}$. No consistent declines in post- versus precontrol periods were noted for summer values of ε_{PAR}.

Transparency was greatest in the lower bay, as indicated by the much lower values for ε_{PAR}. The majority of values ranged from 0.40 to $0.80 \cdot m^{-1}$ (Z_{eu} = 11.5–5.8 m), with no distinct seasonal trends evident. In contrast with the other parts of the bay, ε_{PAR} was often highest during May and early June in the lower bay. Values fluctuated during the summer and increased slightly during late August or early September in some years. There was no change in ε_{PAR} for the postcontrol compared with the precontrol period during any part of the season.

Integral Primary Production

Primary production profiles from the incubator usually showed the classic shape obtained with the in situ technique. Surface rates (unfiltered chamber) were often photoinhibited, with the light-saturated region well defined in two to four of the chambers, depending on light intensity. Rates declined exponentially with depth, and rates from the two chambers with lowest transmission (3 and 10%) usually occurred in this part of the profile. Except on extremely overcast days, rates from the last chamber were greater than zero, so profiles were always extrapolated to the depth of Z_{eu}. Profiles were not always accurately defined in the linear part of the photosynthesis–irradiance profile, particularly on bright days when only one rate (3% chamber) fell in this part of the curve. Also, profiles were not as accurate in the early part of the season in the lower bay when production rates were very low at some depths. Overall, estimates of integral primary production were reasonably accurate. The model of Talling (1957),

$$\Sigma A = \frac{A_{max}}{\varepsilon_{min} \cdot a} \cdot \ln \frac{I'_0}{0.5 I_K},$$

is known to show good agreement with hourly integral rates obtained with the in situ method (Rodhe 1965; Jewson 1976; Jones 1977). We also found good agreement (r = 0.93, n = 1578) between the model and the incubator method: ΣA model = 1.422 + 0.996 ΣA incubator. The low intercept and slope of almost 1.0 indicates that our method provided reasonably accurate estimates of integral primary production.

Values for A_{max} were much higher in the upper than the lower bay because of the higher standing crops, but Z_{eu} was greatly reduced due to high light extinction (Fig. 5). In comparison, the lower bay lacked the extremes of standing crop and production on a volume basis, but the upper to lower bay gradient was reduced when these parameters were integrated over Z_{eu}. Consequently, seasonal trends and differences between years and stations in ΣA were not as evident as with A_{max}, ε_{PAR}, and Chl *a* (Fig. 6).

In the upper bay, monthly means for ΣA were lowest in May (87–129 mg $C \cdot m^{-2} \cdot h^{-1}$) and June (164–222 mg $C \cdot m^{-2} \cdot h^{-1}$ during precontrol years, declining below these ranges in postcontrol years. Integral production increased substantially in July and August, particularly before P control. The value of ΣA was often greater than 300 mg $C \cdot m^{-2} \cdot h^{-1}$ at this time and in 1973 was over 400 mg $C \cdot m^{-2} \cdot h^{-1}$ for both months. In precontrol years, $\Sigma\Sigma A$ averaged 3.50–4.00 g $C \cdot m^{-2} \cdot d^{-1}$ in July and August and was over 5.00 g

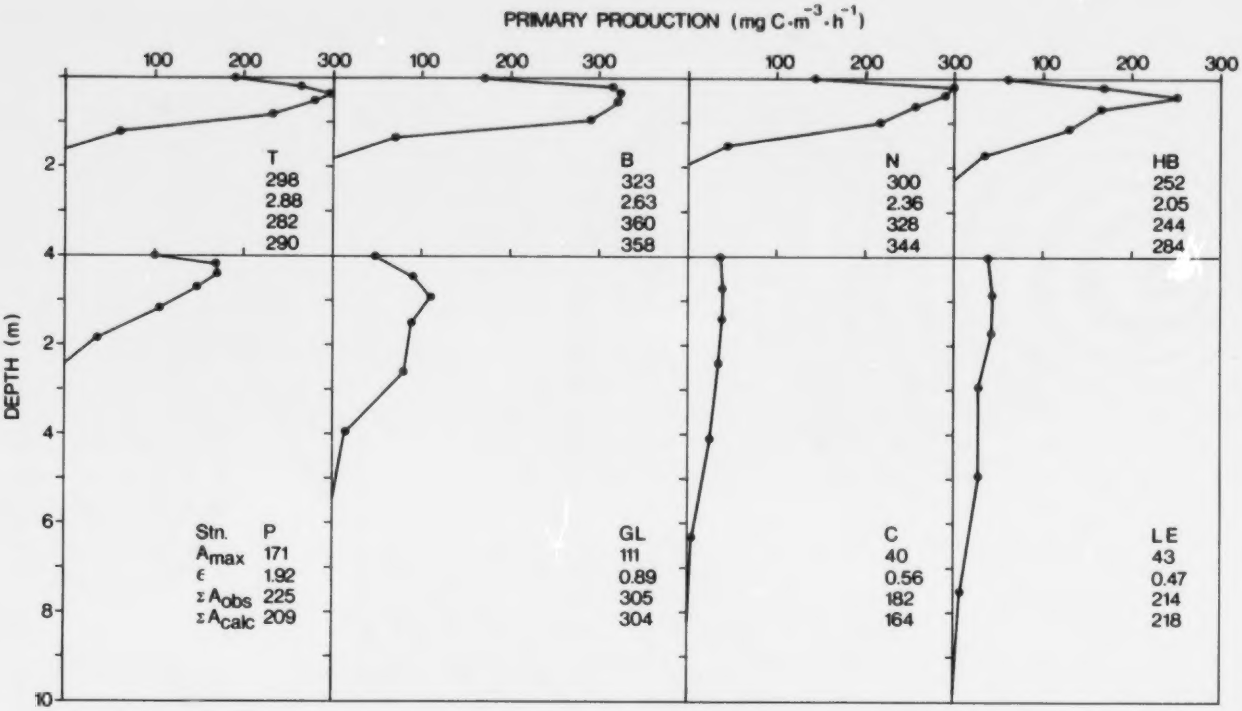

FIG. 5. Comparative depth profiles of primary production at all stations in the Bay of Quinte for the period August 5–8, 1975.

$\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ in July 1973. However, in postcontrol years, ΣA was often less than 200 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ and $\Sigma\Sigma A$ declined (~ 40%) in July and August.

Values for ΣA during May in the middle bay were similar to the upper bay in both pre- and postcontrol periods (53–143 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$). A slight decline was noted in postcontrol (95–155 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$) compared with the precontrol period (140–196 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$) in June. Daily rates showed little change in May and June during the study at the middle bay, averaging 1.00 and 1.60 g $\mathrm{C \cdot m^{-2} \cdot d^{-1}}$ for these months, respectively. As in the upper bay, ΣA increased markedly from July to September. In precontrol years, ΣA was usually over 220 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ and often exceeded 300 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ in these months. However, monthly mean ΣA exceeded 200 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ during July in only one postcontrol year (1981) and was less than 300 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ for August in all postcontrol years except 1980. Values of $\Sigma\Sigma A$ declined 40, 25, and 20% from precontrol monthly means of 2.79, 3.09, and 2.49 g $\mathrm{C \cdot m^{-2} \cdot d^{-1}}$ in July, August, and September, respectively, for the postcontrol period in the middle bay.

The value of ΣA in the lower bay during May was similar to the other regions. In June, ΣA increased but rates were lower than at other stations, with monthly means ranging from 94 to 150 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ in precontrol years. In June of two postcontrol years (1978 and 1980), ΣA was less than 75 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$. The value of $\Sigma\Sigma A$ was similar in the lower bay in May and June to that in other parts of the bay. Levels of ΣA did not increase as rapidly during July as at other locations. Highest rates for ΣA in the lower bay occurred in August and September in most years. Maximum values for ΣA showed little change over the entire study, exceeding a monthly mean of 300 mg $\mathrm{C \cdot m^{-2} \cdot h^{-1}}$ on only one occasion. The range in monthly means for ΣA from July through September overlapped the pre- and postcontrol periods, but the lowest monthly means for ΣA occurred in the postcontrol period in the lower bay. Values for $\Sigma\Sigma A$ were similar to those in the middle bay in both pre- and postcontrol periods from July to September.

Seasonal Gross Primary Production

The total production for the season (g $\mathrm{C \cdot m^{-2}}$) was estimated by integrating the area enclosed by the plot of weekly estimates of $\Sigma\Sigma A$ (Table 2). The length of the season differed slightly between years, but most started May 1 and ended October 1, running 22–24 wk. The differences in season length were slight and were usually the result of different starting or ending times (May, October). The effect of P removal was most noticeable on summer means and maxima, so it is unlikely that these differences in season length were very important in noting differences between pre- and postcontrol periods. The effect of P removal on seasonal gross production was most pronounced in the upper bay. As noted previously for other parameters, 1973 and 1975 were the most productive years, with seasonal production of about 500 g $\mathrm{C \cdot m^{-2}}$. At station B, gross production in all seasons during the precontrol period exceeded 350 $\mathrm{C \cdot m^{-2}}$. In contrast, seasonal production was 306 g $\mathrm{C \cdot m^{-2}}$ during the highest postcontrol season, 1978. The low value for 1981 may be an underestimate because data for $\Sigma\Sigma A$ were unavailable for July. The accuracy of a production estimate of 44.0 g $\mathrm{C \cdot m^{-2}}$ for July obtained by extrapolating from July 1 to August 4 is certainly suspect. However, the ratio A_{max}/ϵ, the principal determinant of integral production (Talling 1965), averaged 62 for the month. This ratio was 58 for July 1980, when data for $\Sigma\Sigma A$ were available weekly and production was estimated at 43.08 g $\mathrm{C \cdot m^{-2}}$. Thus the low seasonal primary production in 1981 may not be in great error and is similar to results in their postcontrol years. The average seasonal gross production for the postcontrol period was 46 and 37% lower than the precontrol

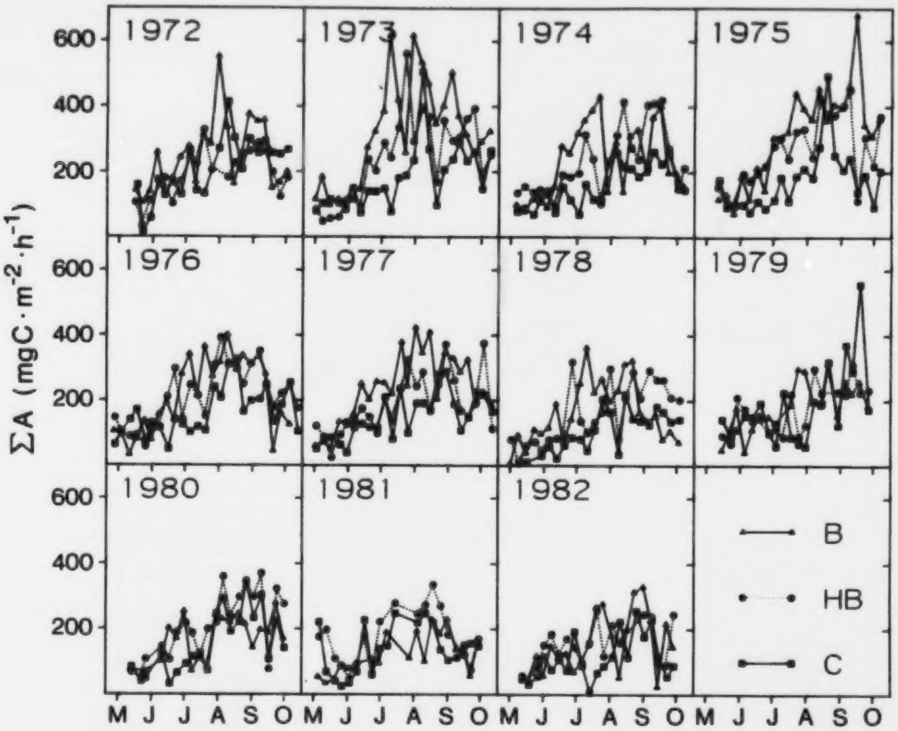

FIG. 6. Season trends in ΣA, the hourly rate of integral primary production, at stations representing the upper (B), middle (HB), and lower (C) Bay of Quinte from 1972 to 1982.

TABLE 2. Total gross primary production (g C · m^{-2}) for the May to September period at eight stations in the Bay of Quinte from 1972 to 1982 (— = not sampled).

Year	T	B	N	HB	P	GL	C	LE
1972	307	404	370	338	390	400	351	—
1973	469	520	501	386	412	417	306	—
1974	273	375	356	350	405	395	289	—
1975	358	514	470	433	431	412	303	323
1976	264	353	320	330	358	394	298	320
1977	317	417	376	344	361	343	318	314
1978	211	306	259	308	338	303	213	239
1979	135[a]	237	289	235	—	272	249	—
1980	167[a]	221	214	284	—	314	243	—
1981	—	194	278	250	—	264	225	—
1982	—	231	242	252	—	254	248	—

[a] Production for June and August.

period at station B and N, respectively. These same averages showed a 26–28% decline in the middle and lower bay. Seasonal gross production at each of the middle and lower bay stations was lower in all postcontrol compared with precontrol years.

Differences Between Years

One-way analysis of variance and Duncan's multiple range test were performed on seasonal means calculated from the weekly data for A_{max}, ε_{PAR}, Chl *a*, and ΣA from the five main stations (B, N, HB, GL, and C).

Changes in seasonal means of these parameters following implementation of P control have been most noticeable in the upper bay (Fig. 7). For example, at station B, A_{max} was significantly higher in all precontrol years compared with each postcontrol year. Similarly, station N had several high production years (1973, 1975, 1977). However, A_{max} was significantly lower in 1974 and 1976 compared with the postcontrol period. At the middle and lower bay locations there was considerable overlap in seasonal means for A_{max} between the two periods. However, like the upper bay, A_{max} in 1973 and 1975 was higher than in all postcontrol years. Differences between the two periods were least evident at station C. Seasonal means at station C from 1973 to 1977 inclusive were significantly higher than only one postcontrol year. The value of A_{max} was most frequently lower in 1978 and 1982 when compared with precontrol years at the middle and lower bay locations.

Interyear comparisons at station B for ε_{PAR} were similar to those for A_{max}. Other than 1972, all precontrol years had significantly higher seasonal means for ε_{PAR} than postcontrol years. There were no significant differences in ε_{PAR} over all years (1972–82) in the middle bay and few in the lower bay.

Only station B showed a consistent difference in ΣA between the two periods. Like A_{max}, seasonal means in ΣA at stations N and HB in 1973 and 1975 were consistently higher than in postcontrol years. All other stations showed considerable overlap between the pre- and postcontrol periods in values of ΣA.

Seasonal means for Chl *a* showed the fewest significant differences between years. Chl *a* was consistently higher in 1973, 1975, and 1977 at station B and in 1973 and 1975 at station N in the upper bay compared with postcontrol years. Few significant differences were noted in Chl *a* levels among years in the middle and lower bay.

Differences Between Stations

The same statistical treatment of data was used to look for groupings of stations within each year. Stations could be

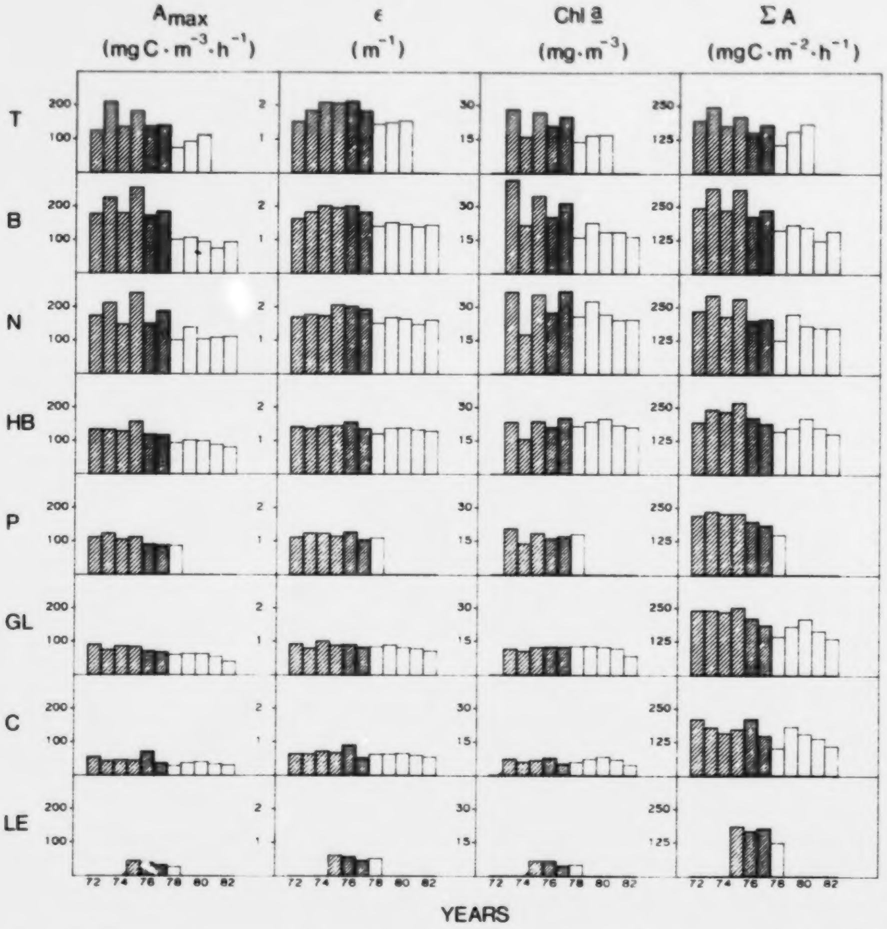

FIG. 7. Histograms of seasonal means for A_{max}, ε_{PAR}, Chl *a*, and ΣA at all stations sampled during the study from 1972 to 1982. Hatched bars represent the pre-P control period, 1972–76, and the white bars represent the postcontrol period, 1977–82.

grouped as representing similar conditions when there was no significant difference in seasonal means for a parameter.

Before P control, a consistent grouping of stations occurred that coincided with the three main regions of the bay. This was particularly evident for ε_{PAR}, which showed distinct groupings and the best upper to lower bay gradient (Millard 1986b). Stations B and N consistently showed no differences for any variables. Station T could often be included, particularly for ε_{PAR}, to form an upper bay grouping. For A_{max} and Chl *a*, station T grouped most frequently with the middle bay stations HB and P. Prior to P control, HB was clearly distinct from the upper bay for ε_{PAR}. Stations HB, P, and GL separated from each other for ε_{PAR}, but station HB consistently grouped with station P and in three years with GL with respect to A_{max} and Chl *a*. Station P was a transition area between the middle (HB) and lower bay (GL). In the lower bay, stations C and LE could be grouped for all variables. Station GL could be grouped with C and LE for a lower bay grouping that encompassed most of Adolphus Reach for A_{max} and Chl *a*. However, GL was usually distinct from the rest of the lower bay with respect to ε_{PAR}. The most distinct groupings of stations for A_{max} occurred in the most productive year, 1975. The only pairs of stations with no significant difference were C–LE and B–N. All other stations were significantly different from one another and from these two groupings.

There were fewer significant differences between stations after P control for the variables directly related to algal biomass (A_{max}, ε_{PAR}, Chl *a*). Consequently, the gradient in productivity from the upper to lower bay was less distinct. This was the case for ΣA throughout the study. Significant differences between regions in the bay occurred less frequently for ΣA than other variables. However, this was even more evident in the postcontrol period when there were almost no significant differences in ΣA between stations in any year.

One of the more notable changes in the postcontrol period was the linking of HB in the middle bay to upper bay stations with respect to A_{max} and Chl *a*. This trend was less evident for ε_{PAR} because station N tended to have higher values for ε_{PAR} although there was no difference between station B in the upper bay and HB. In the postcontrol period there appeared to be only two distinct regions, the upper and middle bay (B, N, and HB) and the lower bay or Adlophus Reach (GL, C).

Relationships

Simple and multiple linear regressions were calculated using monthly means (1972–81) because weekly data for flow and P loading were unavailable (Table 3). The change in importance of certain independent variables from upper and lower bay was

TABLE 3. Results of regressions using monthly means for important variables ([P] = $mg \cdot m^{-3}$; ln flow = $10^6 m^3 \cdot d^{-1}$; TL and PSL = $mg\ P \cdot m^{-2} \cdot d^{-1}$; ns = nonsignificant).

Stations	Dependent variable	a	V_1	b_1	R^2	V_2	b_2	R^2	Regression F-value	R^2 (%)
B	$\Sigma\Sigma A$	21.16	ΣA	10.32	86.8				316.92	86.8
HB		219.17		9.40	87.3				330.76	87.3
C		445.14		8.80	82.8				231.76	82.8
B, HB, C		246.90		9.48	85.9				901.09	85.89
B	ΣA	−9.11	$A_{max}/\varepsilon_{PAR}$	2.68	95.2				948.96	95.2
HB		7.58		2.52	88.3				362.59	88.3
C		−0.96		2.52	85.6				284.55	85.6
B, HB, C		−9.11		2.68	95.2				948.96	95.2
B	A_{max}	−94.24	Chl *a*	4.02	67.1	Temperature	7.38	4.8	53.76	71.9
HB		19.04		4.31	63.6		ns	—	75.11	63.6
C		−4.30		2.44	15.3		2.04	59.8	63.18	75.1
B	ε_{PAR}	1.14	Chl *a*	0.022	62.9				73.1	62.9
HB		0.87		0.023	71.4				107.2	71.4
C		—		ns	—				—	—
B	Chl *a*	−8.96	[P]	0.53	71.3	Temperature	ns	—	106.6	71.3
HB		−28.15	[P]	0.46	40.2		1.56	15.6	17.3	55.8
C		−4.08	ln flow	1.67	13.3		0.48	17.1	9.2	30.4
B	[P]	107.17	TL	ns	—	ln flow	−20.66	37.4	28.73	37.4
HB				ns	—		ns	—	—	—
C				ns	—		ns	—	—	—
B	[P]	74.3	PSL	51.03	25.6	ln flow	−19.52	37.4	40.15	63.1
HB		0.041		0.03	21.0		−0.005	6.2	8.8	27.2
C				ns	—		ns	—	—	—
B	ΣA	272.16	PSL	167.72	21.2	ln flow	−76.59	43.3	42.77	64.5
HB		278.51		80.83	7.2		−60.95	38.8	20.01	46.0
C		199.58		59.57	5.6		−37.95	21.5	8.72	27.1
B	A_{max}	199.43	PSL	181.01	26.7	ln flow	−75.19	45.6	61.55	72.4
HB		145.35		75.83	10.9		−38.73	27.6	14.70	38.5
C		40.27		18.40	11.8		−5.70	8.9	6.13	20.7

shown by using data from stations B, HB, and C. In some cases, variables were significant in one region of the bay but not in another and this has been indicated. Certain variables were used as both dependent and independent because a progression of cause–effect links was formed. For example, in the upper bay, Chl *a* was dependent on total P concentrations ([P]) which were best explained by flow and point-source P loading (PSL). The two regressions could have been replaced by one relating Chl *a* to flow and point-source P loading, but the influence of these variables is expressed through [P] so the progressive dependence has been shown. Observed values of ΣA and those predicted by Talling's model agreed very closely (Millard 1986b). As a result, measured ΣA explained much of the variance of $\Sigma\Sigma A$ and was related to day rates through the day length.

Similar values for the multiple correlation coefficient (R^2) were obtained throughout the bay for the regression of A_{max} versus Chl *a* and temperature. However, the role of each variable differed markedly between the upper and lower bay. Temperature explained only a small part of the variance in A_{max} in the upper bay compared with Chl *a*, while in the lower bay the relative importance was reversed.

In the upper bay, Chl *a* was closely related to [P], but the relationship deteriorates from upper to lower bay. In fact, at station C, [P] was not a significant explanatory variable for Chl *a*. Temperature had a similar effect on the total R^2 with Chl *a* in both the middle and lower bay. In the lower bay, ln flow was positively related to Chl *a* because levels were often higher in the spring when river flows were highest. The influence of flow may have been direct because flushing was rapid enough that either algal biomass or [P] required for growth was exported from the upper bay and could have increased levels of either variable in the lower bay.

Total P loadings (TL = rivers + point-source) did not contribute significantly to regressions with [P] because they were highly correlated with river flows (r = 0.93) which had a negative influence on [P]. On the other hand, the combination of PSL (25.6%) and ln flow (37.4%) explained 63.1% of the variance in [P] in the upper bay. In the middle bay, PSL had a similar influence, while ln flow was significant, but explained only 6.2% of the variance in [P]. In contrast, neither of these variables was a significant predictive variable for [P] in the lower bay. Similar to [P], much of the variance in A_{max} (72.4%) and ΣA (64.5%) was explained by ln flow and PSL, indicating that the effect was through [P].

Discussion

The extreme eutrophy of the upper Bay of Quinte prior to P removal was evident when compared with other parts of the Great Lakes and productive lakes worldwide (Table 4). From 1972 to 1977, the upper bay was probably the most productive embayment in the Great Lakes. Primary production rates and Chl *a* equalled some of the most eutrophic temperate-climate lakes documented in the literature. However, the extreme productivity of Ethiopian soda lakes greatly exceeds that of lakes in temperate regions.

The reductions following P control in summer levels of primary production and Chl *a* were undoubtedly due to the reduc-

TABLE 4. Comparison of maximum values of Chl *a* and primary production[a] in the Bay of Quinte with other eutrophic lakes.

	Chl *a* ($mg \cdot m^{-3}$)	A_{max} ($mg\,C \cdot m^{-3} \cdot h^{-1}$)	ΣA ($mg\,C \cdot m^{-2} \cdot h^{-1}$)	$\Sigma\Sigma A$ ($g\,C \cdot m^{-2} \cdot d^{-1}$)	Reference
Great Lakes					
Lake Ontario inshore	13–14	24	120	1.08	Glooschenko et al. 1974
Bay of Quinte					
Station B	140	472	679	7.60	This study
Station HB	66	397	561	6.20	
Station C	20	147	505	5.50	
Hamilton Harbour	50	160	220	—	Harris et al. 1980
Lake Huron Saginaw Bay	67	158	—	—	Munawar and Munawar 1982
Lake Erie western basin	20	150	400	4.76	Glooschenko et al. 1974
Temperature-climate lakes					
Lake 227, ELA Canada	180	—	—	2.90	Schindler and Fee 1973
Lake Minnetonka, Minnesota	60	300–560	—	4.00–7.60	Megard 1972
Lough Neagh, Ireland					
Kinnego Bay	300	585	420	4.30	Jewson 1976
Loch Leven, Scotland	200	300–350	480	6.30	Bindloss 1974, 1976
Lake Norrvikken, Sweden	100–400	400–600	—	3.98	Ahlgren 1970
Lake Vombsjön, Sweden	75–100	450	550	4.50	Gelin 1975
African lakes					
Lake George, Uganda	1000	1500	660	3.00–5.00	Ganf 1974, 1975
Lake McIlwaine, South Africa	95	653	635	6.03	Robarts 1979
Lake Elmenteita, Kenya	367	594	167	1.78	Melack and Kilham 1974; Kalff 1983
Lake Aranguadi, Ethiopia	2170	8919	546	17.1[b]	Talling et al. 1973, table 1
Lake Kilotes, Ethiopia	412	3041	720	3.72[b]	Talling et al. 1973, table 1

[a] Results from studies using oxygen methods were converted to C uptake using a photosynthetic quotient of 1.25.

[b] Calculated from diurnal measurements of in situ oxygen concentration.

TABLE 5. July–August means (1972–81) for primary production ($\Sigma\Sigma A$, A_{max}), Chl *a*, P loading and concentration [P], river flow, daily radiation (I_o), and water temperature at station B (P loading = $mg \cdot m^{-2} \cdot d^{-1}$; flow = $10^6\,m^3 \cdot d^{-1}$; I_o = total solar radiation = $g\,cal \cdot cm^{-2} \cdot d^{-1}$).

				P loading					
Year	$\Sigma\Sigma A$	A_{max}	Chl *a*	Total	Point source	[P]	Flow	I_o	Temperature (°C)
1972	3512	210	—	2.80	0.91	72	13.4	459	22.4
1973	4577	337	46	1.51	0.74	108	4.28	480	24.3
1974	3137	224	22	1.33	0.65	85	5.21	491	22.7
1975	4256	341	44	1.41	1.02	105	2.18	487	23.6
1976	3256	266	37	1.79	0.85	91	5.69	446	22.0
1977	3530	286	47	1.04	0.68	101	2.36	482	22.6
1978	3011	156	22	0.58	0.29	53	2.01	502	23.6
1979	2053	139	32	0.94	0.22	52	3.62	471	22.2
1980	1880	124	22	1.17	0.26	52	9.30	471	23.3
1981	1795	109	28	1.00	0.31	54	5.99	463	23.9

tion in PSL. Average PSL was reduced 67% resulting in declines of 46 and 37% at stations B and N, respectively, in seasonal gross primary production in the post-P control period (Table 5). TL did not show the same reduction because of the influence of river loadings (TL–PSL) which showed no consistent trend over the study period. Flow had a moderating effect on [P] through dilution and helped offset the effects of low-flow, high-concentration PSL (Johnson and Owen 1971; Minns et al. 1986). As a result, river P loadings had little net effect on [P] because they were highly correlated with flow, although they were equal to or greater than PSL in some years, i.e. 1973 and 1979. This explains why TL was not significant in regressions with [P]. High PSL in the upper bay coupled with lower summer flows caused the summer increase in [P]. It is not surprising, then, that the most productive seasons (1973, 1975, 1977) were years when the July–August PSL were highest and flows low. In constrast, PSL were similar in the other precontrol years (1972, 1974, 1976), but flows were higher. It is interesting that in 1973 neither PSL nor flow was as extreme as in 1975, yet $\Sigma\Sigma A$, A_{max}, and Chl *a* were as high. It is possible that higher temperature and extended periods of hot sunny weather may have contributed to the high productivity. Flow explained a greater part of the variance in [P] than PSL. However, the limiting effect of PSL below some threshold was evident in 1978. During this first season of P control, summer flows were the lowest observed during the study, yet marked reductions in primary production and Chl *a* were observed.

In addition to its dilution of [P], flow influenced biomass dynamics as a direct loss factor in April and May. At this time, 5–12% $\cdot d^{-1}$ of the standing crop was exported via outflow. Furthermore, the high spring flow reduced the gradient in [P] from upper to lower bay compared with the summer because of the direct influence of upper bay water. As flows subsided during the summer, the two regions became dissimilar because concentrations in the lower bay were diluted by intrusions of low-concentration Lake Ontario water (Minns et al. 1986). This may explain why neither flow, TL, nor PSL explained any of the variance in [P] in the lower bay. The lower Chl *a* in the lower bay is likely due to the lower [P] although a significant relationship between these two variables for station C data alone did not exist.

Despite the reductions in [P], conditions are still eutrophic in the upper bay. Summer [P] remained high (40–60 $\mu g \cdot L^{-1}$) after P control started, but values over 80 $\mu g \cdot L^{-1}$ have been rare since 1978. Furthermore, over 35% of the variance in [P] was unexplained by flow and PSL, suggesting that other factors, such as sediment P regeneration, were important in P supply in the upper bay. Millard (1986a) found that by late June 1978, turnover times for orthophosphate were rapid, with uptake dominated by bacteria-sized particles. This type of situation indicated that the entire seston including algae was P limited (Lean et al. 1983; Lean 1984). During that season, Millard found that the proportion of total phosphate uptake by larger particles increased by late July as total biomass and that of larger algae increased (Nicholls et al. 1986). These changes indicated that P supply increased, probably from sediment regeneration. In the short term, large algae become increasingly important in P uptake as P levels increase (Lean and White 1983; Lean 1984) and large algae often dominate communities when nutrient supply is high (Parsons and Takahashi 1973). PSL showed little seasonal variation, but accounted for part of the summer increase in [P] because of a buildup as flows declined during the summer. However, at the lower PSL since 1978, calculations showed that [P] should have decreased during the summer if there had been no sediment regeneration (C. K. Minns, pers. comm.). This decline in summer [P] could have occurred because sedimentation losses would have been greater than the usual increase in [P] at lower flow.

The timing and magnitude of summer peaks in phytoplankton biomass were probably linked to seasonal patterns in internal P loading from the sediments. Calculated regeneration rates of P were high in the upper bay, often exceeding external inputs (Minns et al. 1986). Research on P dynamics in limnocorrals in the upper bay also showed that regeneration rates could be high (Lean and Charlton 1976). Millard (1976) suggested that in the limnocorrals, sediment regeneration of P was part of a positive-feedback cycle that was triggered by production and sedimentation of organic matter. In this cycle, the initial development of biomass in the spring and early summer was driven by external P loading. The triggering effect for regeneration was probably the loss of the thin oxygenated microzone at the sediment surface. Sediments in the upper bay are both enriched with P and highly reduced (Damiani and Thomas 1974; Minns et al. 1986). A period of calm weather coupled with high seston levels could have caused increased sedimentation, loss of oxygen at the sediment surface through decomposition and respiration, and diffusive release of soluble P. Also, calm weather would have reduced circulation and renewal of oxygen at the sediment surface. Once regeneration was triggered, algal biomass became uncoupled from external P loading because of the vast internal supply of P. Lowering external P loading reduced the early development of standing crops that could sediment and trigger P release. The trend to later and less drastic peaks in P concentrations, production, and biomass may have been the result of delayed regeneration as a result of reduced PSL. Other modes of P regeneration such as disturbance of sediments during windy weather may have also been in effect simultaneously (Wright 1976). In the upper Bay of Quinte, the role of sediments in nutrient regeneration must be considered as a critical factor limiting the rate of recovery.

One of the most striking features about the Bay of Quinte was the distinct gradient from upper to lower bay in [P] and volume-based measurements of algal standing crops and production. Although the smaller algal densities in the lower bay were partially the result of lower [P], other factors such as lower temperature, deep vertical mixing, and intrusion of lake water were important in this part of the bay (Millard 1986b; Freeman and Prinsenberg 1986). In contrast, ΣA was remarkably similar throughout the bay, a consequence of strong self-shading properties of the phytoplankton communities in the upper bay. The ratio $A_{max} / \varepsilon_{PAR}$ which explained much of the variance in ΣA is known to be a stabilizing determinant of integral production (Talling 1965). As a result, less than proportionate increases in ΣA occur in response to changes in standing crop (Talling 1965; Harris et al. 1980). For example, the coefficient of variation for this expression was only 19.6% compared with 60.9% for A_{max} using the data from Fig. 5. As algal crops increased, the negative effect of self-shading was an increase in ε_{PAR} and shortening of the euphotic zone. However, biomass increases also caused higher A_{max} and thus, $A_{max} / \varepsilon_{PAR}$ remained fairly constant. In contrast, at the lower phytoplankton densities found in the lower bay, euphotic zone depths were greater but A_{max} was reduced.

Chl *a* was a dominant factor in light extinction in the upper and middle bay, a prerequisite for high photosynthetic yields per unit area (Bannister 1974). Although detailed aspects of the ε_{PAR} versus Chl *a* relationship are presented elsewhere (Millard 1986b), it is worth noting that both background light extinction (intercept, ε_{PAR} versus Chl *a*) and the incremental effect changes in Chl *a* have on ε_{PAR} (slope) were high in the Bay of Quinte compared with other waters (Bindloss 1976; Jewson 1976). High values for these parameters reduced the size of algal standing crops in Z_{eu}, thereby limiting potential photosynthetic yields.

Mean monthly radiation in our study did not contribute significantly in regressions with Chl *a* and A_{max} as the dependent variable. This was the result of the small variance in monthly radiation over the study (1972–82). There has been no significant difference between years in mean seasonal radiation (May–September inclusive) during the study. The most productive months (July–August) had coefficients of variation of 6.9 and 3.5%, respectively, for the average over the study of the mean radiation for each of these months. In the other months (May, June, September), about 80% of the monthly means were within 10% of the grand mean for the respective month over all years. Of course, irradiance was highly variable on a shorter time scale of hours to days. Variability in irradiance was probably most important when fluctuations were more rapid than the time requried for phytoplankton populations to adapt to a changing light regime (Harris et al. 1980). In the Bay of Quinte, PSL and flushing rates were much more important factors in determining seasonal production than meteorological factors such as irradiance and temperature. In a global analysis of factors affecting production, Schindler (1978) similarly concluded that flushing and P loading, not radiation, were the keys to controlling eutrophication. In the upper Bay of Quinte, sediment regeneration of P is also an important factor governing productivity.

References

AHLGREN, G. 1970. Limnological studies of Lake Norrviken, a eutrophicated Swedish lake. II. Phytoplankton and its production. Schweiz. Z. Hydrol. 32: 353–394.

Ahlgren, I. 1977. Role of sediments in the process of recovery of a eutrophicated lake, p. 372–377. *In* H. L. Golterman [ed.] Interactions between sediments and freshwater. Dr. W. Junk bv Publishers, The Hague. 473 p.

Bannister, T. T. 1974. Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnol. Oceanogr. 19: 1–12.

Bindloss, M. E. 1974. Primary productivity of phytoplankton in Loch Leven, Kinross. Proc. R. Soc. Edinb. Sect. B (Biol. Sci.) 74: 157–181.

1976. The light climate of Loch Leven, a shallow Scottish Lake, in relation to primary production by phytoplankton. Freshwater Biol. 6: 501–518.

Damiani, V., and R. L. Thomas. 1974. The surficial sediments of the Big Bay section of the Bay of Quinte, Lake Ontario. Can. J. Earth Sci. 11: 1562–1576.

Dillon, P. J., K. H. Nicholls, and G. W. Robinson. 1978. Phosphorus removal at Gravenhurst Bay, Ontario: an 8 year study on water quality changes. Verh. Int. Ver. Limnol. 20: 263–271.

Edmondson, W. T. 1977. Recovery of Lake Washington from eutrophication, p. 102–109. *In* J. Cairns, Jr., K. L. Dickson, and E. E. Henicks [ed.] Recovery and restoration of damaged ecosystems. University of Virginia Press, Charlottesville, VA.

Environment Canada. 1979. Analytical methods manual. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

Forsberg, C. 1979. Responses to advanced wastewater treatment and sewage diversion. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13: 278–292.

Freeman, N. G., and S. J. Prinsenberg. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Ganf, G. G. 1974. Incident solar irradiance and underwater light penetration as factors controlling the chlorophyll *a* content of a shallow equatorial lake (Lake George, Uganda). J. Ecol. 62: 593–610.

1975. Photosynthetic production and irradiance–photosynthesis relationships of the phytoplankton from a shallow equatorial lake (Lake George, Uganda). Oecologia 18: 165–183.

Gelin, C. 1975. Nutrients, biomass and primary productivity of nannoplankton in eutrophic Lake Vombsjön, Sweden. Oikos 26: 121–139.

Glooschenko, W. A., J. E. Moore, M. Munawar, and R. A. Vollenweider. 1974. Primary production in Lakes Ontario and Erie: a comparative study. J. Fish. Res. Board Can. 31: 253–263.

Harris, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. Can. J. Fish. Aquat. Sci. 37: 877–900.

Harris, G. P., G. D. Haffner, and B. B. Piccinin. 1980. Physical variability and phytoplankton communities. II. Primary productivity by phytoplankton in a physically variable environment. Arch. Hydrobiol. 88: 393–425.

Jewson, D. H. 1976. The interaction of components controlling net phytoplankton photosynthesis in a well-mixed lake (Lough Neagh, Northern Ireland). Freshwater Biol. 6: 551–576.

Johnson, M. G., and D. A. Hurley. 1986. Overview of Project Quinte — 1972–1982, p. 1–6. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G., and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

Jones, R. I. 1977. Factors controlling phytoplankton production and succession in a highly eutrophic lake (Kinnego Bay, Lough Neagh). II. Phytoplankton production and its chief determinants. J. Ecol. 65: 561–577.

Kalff, J. 1983. Phosphorus limitation in some tropical African lakes. Hydrobiologia 100: 101–112.

Larsen, D. P., J. Van Sickle, J. W. Malueg, and P. D. Smith. 1979. The effect of wastewater phosphorus removal on Shagawa Lake, Minnesota: phosphorus supplies, lake phosphorus and chlorophyll *a*. Water Res. 13: 1259–1272.

Lean, D. R. S. 1984. Metabolic indicators for phosphorus limitation. Verh. Int. Ver. Limnol. 22: 211–218.

Lean, D. R. S., A. P. Abbott, M. N. Charlton, and S. S. Rao. 1983. Seasonal phosphate demand for Lake Erie plankton. J. Great Lakes Res. 9: 83–91.

Lean, D. R. S., and M. N. Charlton. 1976. A study of phosphorus kinetics in a lake ecosystem, p. 283–294. *In* J. O. Nriagu [ed.] Environmental biochemistry. I. Ann Arbor Science Publishers, Ann Arbor, MI.

Lean, D. R. S., and E. White. 1983. Chemical and radiotracer measurements of phosphorus uptake by lake plankton. Can. J. Fish. Aquat. Sci. 40: 147–155.

Likens, G. E. [ed.] 1972. Nutrients and eutrophication: the limiting-nutrient controversy. Spec. Symp. Am. Soc. Limnol. Oceanogr. 328 p.

Long, E. B., and G. D. Cooke. 1972. A quantitative comparison of pigment extraction by membrane and glass-fiber filters. Limnol. Oceanogr. 16: 990–992.

Megard, R.O. 1972. Phytoplankton, photosynthesis and phosphorus in Lake Minnetonka, Minnesota. Limnol. Oceanogr. 17: 68–87.

Melack, J. M. and P. Kilham. 1974. Photosynthetic rates of phytoplankton in East African, saline lakes. Limnol. Oceanogr. 19: 743–755.

Millard, E. S. 1976. Self-regulatory interactions in enclosed phytoplankton communities subjected to different nutrient loadings. M.Sc. thesis, University of Guelph, Guelph, Ont. 173 p.

Millard, E. S. 1986a. Seasonal trends in turnover times of orthophosphate in the Bay of Quinte, Lake Ontario, p. 91–99. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. Effect of light climate, photosynthetic capacity, and respiration on gross integral primary production and net primary production potential in the Bay of Quinte, Lake Ontario, p. 128–138. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Ministry of the Environment. 1981. Outlines of analytical methods. Laboratory Services Branch, Rexdale, Ont. 246 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosophorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Munawar, M., and I. F. Munawar. 1982. Phychological studies in lakes Ontario, Erie, Huron and Superior. Can. J. Bot. 60: 1837–1858.

Nicholls, K. H., L. Heintsch, E. C. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosophorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Parsons, T. R., and M. Takahashi. 1973. Environmental control of phytoplankton cell size. Limnol. Oceanogr. 18: 511–515.

Robarts, R.D. 1979. Underwater light penetration, chlorophyll *a* and primary production in a tropical African lake (Lake McIlwaine, Rhodesia). Arch. Hydrobiol. 86: 423–444.

Rodhe, W. 1965. Standard correlations between pelagic photosynthesis and light, p. 365–382. *In* C. R. Goldman [ed.] Primary productivity in aquatic environments. Mem. Ist. Ital. Idrobiol. 18 (Suppl.). University of California Press, Berkeley, CA.

1969. Crystallization of eutrophication concepts in Northern Europe, p. 50–64. *In* Eutrophication: causes: consequences, correctives. National Academy of Sciences, Washington, DC.

Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. Limnol. Oceanogr. 1: 61–70.

Schindler, D. W. 1971. Carbon, nitrogen, and phosphorus and the eutrophication of freshwater lakes. J. Phycol. 7: 321–329.

1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnol. Oceanogr. 23: 478–486.

Schindler, D. W., and E. J. Fee. 1973. Diurnal variation of dissolved inorganic carbon and its use in estimating primary production and CO_2 invasion in lake 227. J. Fish. Res. Board Can. 30: 1501–1510.

Schindler, D. W., H. Kling, R. V. Schmidt, J. Prokopowich, V. E. Frost, R. A. Reid, and M. Capel. 1973. Eutrophication of lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

Smithsonian Institution. 1951. Smithsonian meteorological tables. 6th ed. Smithsonian Institution, Washington, DC.

Sonzogni, W. C., G. P. Fitzgerald, and G. F. Lee. 1974. Effects of wastewater diversion on the lower Madison lakes. J. Water Pollut. Control Fed. 47: 535–542.

Talling, J. F. 1957. The phytoplankton population as a compound photosynthetic system. New Phytol. 56: 133–149.

1965. The photosynthetic activity of phytoplankton in East African lakes. Int. Rev. Gesamten Hydrobiol. 50: 1–32.

Talling, J. F., R. B. Woods, M. V. Prosser, and R. M. Baxter. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. Freshwater Biol. 3: 53–76.

VOLLENWEIDER, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD Tech. Rep. DAS/CS1/68.27: 182 p.

1974. A manual on methods for measuring primary production in aquatic environments. IBP Handb. No. 12. Blackwell Scientific Publications, Oxford. 213 p.

WRIGHT, D. G. 1976. Wind induced regeneration of phosphorus from the sediments of the upper Bay of Quinte. M.Sc. thesis, University of Guelph, Guelph, Ont. 62 p.

Aquatic Macrophytes in the Bay of Quinte, 1972–82

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Crowder, A., and M. Bristow. 1986. Aquatic macrophytes in the Bay of Quinte, 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario, Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

By 1972, eutrophication had caused a shallow euphotic zone, limiting the area of submerged macrophytes to 2 m depth in the upper bay and 4 m near Lake Ontario. In the 1950s, smaller algal biomass had been associated with deeper, larger weedbeds. Standing crop, species richness, and cover were relatively low throughout the Bay in 1972–82, particularly in the Belleville–Big Bay region. Following phosphorus control, cover increased in 1979, but decreased in 1982. In Hay Bay, species richness decreased and chlorophyll *a* in the water column increased after phosphorus control. Concurrently with eutrophication, *Myriophyllum spicatum* invaded and become a dominant plant in the submerged community. Phosphate in standing crops of submerged macrophytes and cattail marshes was estimated in 1979.

En 1972, l'eutrophisation avait créé une zone euphotique peu profonde, limitant le secteur où se trouvent les macrophytes submergés à 2 m dans la partie supérieure de la baie et à 4 m près du lac Ontario. Dans les années 1950, à une plus faible biomasse des algues correspondaient des lits de végétation plus profonds et plus importants. La biomasse, la diversité des espèces et le couvert ont été relativement faibles dans toute la baie entre 1972 et 1982, spécialement dans la région de Belleville–baie Big. Suite à la limitation du phosphore, le couvert a augmenté en 1979, mais a diminué en 1982. Dans la baie Hay, la diversité des espèces a diminué et la quantité de chlorophylle *a* dans la colonne d'eau a augmenté après qu'on eût réduit les apports de phosphore. En même temps que l'eutrophication, il y a eu invasion de *Myriophyllum spicatum*, qui est devenu une plante dominante dans la communauté des plantes submergées. On a évalué en 1979 le phosphate présent dans la biomasse des macrophytes submergées et des marais à quenouilles.

Introduction

Extensive wetlands dominated by emergent plants alternate with bare rocky shores to form the shoreline of the Bay of Quinte, with submerged weekbeds extending offshore in some areas. When phosphorus control was instituted in the 1970s, it was known that submerged weed beds had been larger and denser in the 1950s and early 1960s, and had declined in the late 1960s (J. Christie and D. Hurley, Glenora Fisheries Station, pers. comm.). Our field work was designed to detect possible changes following control of point sources of phosphorus, in community composition, diversity, cover, and standing crop of submerged plants.

The three topics of this paper are (1) evidence of changes in macrophytes prior to 1971, (2) changes during 1972–82, and (3) an estimate of the magnitude of the phosphorus pool in the standing crop of emergent and submergent plants in 1979. Such an estimate is essential for future numerical modelling of the ecosystem. An benchmark data, types of reproduction and the stem length of one species were recorded.

Since Project Quinte began, changes in species richness and biomass have been described in several lakes during eutrophication. Generally, enrichment leads at first to increased macrophytic growth, but water opacity due to algal growth and/or turbidity later causes a decline in weedbeds (Bannister and Bubeck 1978; Best 1982; Eaton and Kardos 1978; Jupp and Spence 1977; Oglesby 1978; Phillips et al. 1978; Schaffner and Oglesby 1978; Spence 1975; Weller 1981). In the Bay of Quinte, algal standing crop is known to have increased during the reported decline in macrophytes (Nicholls et al. 1986). The same trends have been observed in both North America and Europe, and the example closest to the Bay of Quinte is the Finger Lakes in New York (Bloomfield 1978).

While the process of eutrophication has been widely described since the 1970s, recovery due to removal of phosphorus has not. We postulated that phosphorus control would decrease algal biomass, leading to better water transparency and to an increase in macrophytes.

Macrophytes prior to 1972

The earliest record of the vegetation is that of John Macoun (1878, 1883–90), who listed 37 aquatic plant species in the Bay, some of which were probably never on the shoreline. Nomenclature in this paper follows Scoggan (1978), and Macoun's usage has been brought up to date. Eighteen of the species were present in 1972–82, including *Najas flexilis*, *Potamogeton illinoensis*, *P. zosterifolius*, *Zannichellia palustris*, *Vallisneria americana*, and *Ceratophyllum demersum* among the submerged plants. Emergent species still in the Bay included *Sparganium eurycarpum*, *Glyceria canadensis*, *Phragmites australis*, and *Cyperus strigosus* Cattail (*Typha latifolia*) was listed by Macoun as common across Canada, and not mentioned specifically in this area. Wild rice, *Zizania aquatica*, was described as "very abundant in the Bay of Quinte."

Plants listed by Macoun as abundant in the Belleville area included *Potamogeton gramineus*, *P. illinoensis*, *P. praelongus*, and *Zannichellia palustris*, none of which were found at Belleville in 1972–82.

Christie and Hurley have described lush weed beds in the 1950s followed by decline in the mid-1960s. A search for quantitive evidence of this trend has been frustrating. The Great Lakes Pilot books (Canadian Hydrographic Service) of 1957 and 1968 described the same weed beds, and these are still extant. While the Ontario Ministry of Environment (OME) is known to have issued large numbers of permits for the destruc-

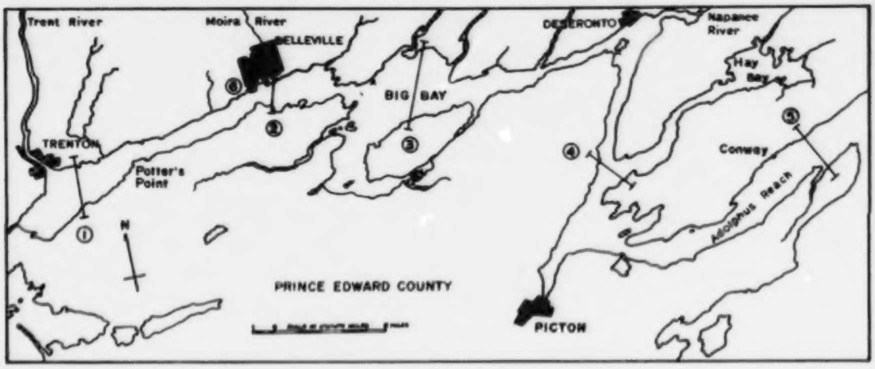

FIG. 1. Sites of transects in the Bay of Quinte, 1972–82.

tion of aquatic weeds in the early 1960s (G. Owen, OME, Kingston, Ont., pers. comm.), records have not survived.

In the 1950s, when marsh habitats for wildlife were described by Peters (1951), stands of wild rice were abundant in Hay Bay. Large stands also grew in the Rossmore–Belleville area at that time (A. Revill, Belleville, Ont., pers. comm.).

To sum up this fragmentary evidence, there seems to have been some loss of species richness over the past century, with the most noticeable change being a loss of rice beds since the 1950s. Areas formerly occupied by rice beds are now dominated by cattails.

Paleoecological records do not shed any light on these changes, although an earlier expansion of cattails occurred some 200 yr ago (Terasmae and Mirynech 1964).

Macrophytes from 1972 to 1982

Methods

Submerged plants were sampled by divers in 1972, 1973, 1974, and after phosphorus control, in 1979 and 1982. Sampling was done twice in the summer, but all results given are from late July, the time of maximum biomass. Species frequencies, species richness, diversity, and cover were calculated from data collected along transects because random sampling points used too much diving time. Transects were located at Trenton (1), Belleville (2), Big Bay (3), Hay Bay (4), and Conway (5) (Fig. 1), in the same locations used for collection of physical, chemical, and algal data (Robinson 1986). At 29-m intervals along each transect, the substrate, depth, and transparency (Secchi disc values) were recorded, since all these influence species composition and abundance. The method of sampling plants was a modified form of point transect (Wood 1975; Smith 1980); 28 knots 1.5 cm in diameter were placed at intervals of 1 m on a line 29 m long. Starting at one shore, the line was staked by the divers at both ends, and any plants touching a knot were collected into a plastic bag. The bags were brought to a boat and the plants identified and counted. Notes on stem length, presence of flowers or winter buds, etc., were made. Then one end of the line was swung around, aligned by compass, and pegged down further along the next section of transect; the process was repeated until the second shore had been reached or until there had been no plants in three consecutive 29-m portions of the transect. In 1972–74, single lines were used; in 1979–82, replicate samples were obtained with parallel transects which the divers tried to keep 1 m apart (the opacity of water sometimes made this difficult). Transects were begun at 0.5 m depth to eliminate areas possibly exposed at low water.

Transects are described as Trenton North (Trenton N), Hay Bay East (Hay Bay E), etc. To obtain comparative values of cover, etc., transects which were not sampled regularly were used at areas inside the bay such as Picton, at Wolfe and Simcoe Islands in Lake Ontario, and at neighbouring lakes in eastern Ontario (Crowder et al. 1977a).

Transect data are less suitable for analysis of species relationships than data from quadrats, but provide a relatively rapid method of making areal or temporal comparisons (Wood 1975). From the transect data, frequency (the percentage of vegetated sampling points at which a particular species occurred), abundance (the number of individuals of all species, expressed as percentages), and cover (the percentage of points covered by any species of plant, as a measure of density) were calculated. Data was analysed using the SPSS package (Nie et al. 1975). Significance was defined as $p < 0.05$. Duncan's and Tukey's tests were used for comparison of means of standing crop.

Diversity was examined using species richness (S) (McNaughton and Wolf 1979) and the Shannon–Wiener index (H') for two inshore transect lines at each site (Smith 1980):

$$H' = \sum_{i=1}^{S} \left(\frac{n_i}{N}\right) \log_2 \left(\frac{n_i}{N}\right).$$

Diversity measures for macrophytes are inexact because of fragmentation of plants and difference in sizes. Lemnaceae, Characeae, and bryophytes were omitted from the calculations.

Similarity between transects in different years and sites was tested using the Jaccard coefficient ($S_j = p/p + m$ where $p =$ positive matches and $m =$ mismatches) (Sokal and Sneath 1973).

Transects were extended into marshes, after phosphorus control, to sample emergent vegetation. The shoreline above 0.5 m depth in areas without marshes were not sampled, resulting in an underestimate of floating-leaved vegetation (*Nymphaea*, *Nurphar*, etc.) and littoral species (*Equisetum fluviatile*, *Scirpus validus*, *Sagittaria* spp., and *Sparganium* spp.).

Results

Substrates

Profiles of transects were shown in Bristow et al. (1977). Limestone was observed along the transects at Trenton S, Belleville N and S, and Big Bay S. Boulders occurred along Trenton N and S, Belleville N, Big Bay N, Hay Bay E, and Conway N.

TABLE 1. Depth of transects, calculated as percentages of sampling points within 0.5-m zones.

Depth (m)	Trenton	Belleville	Big Bay	Hay Bay	Conway
0.5–1	10	6	12	11	9
1.1–1.5	27	11	21	24	11
1.6–2.0	34	11	28	25	11
2.1–2.5	19	24	14	17	20
2.6–3.0	10	15	9	12	12
3.1–3.5	4	8	5	4	12
3.6–4.0	0	7	2	3	6
4.0 +	4	17	9	5	18

TABLE 2. Means of Secchi disc measurements (m) made at 29-m intervals along each of five transects in July during four years of the decade 1972–82. Means for each site combining the four years and for each year combining all sites are also given.

	Trenton	Belleville	Big Bay	Hay Bay	Conway	Bay of Quinte Mean
1972	1.1	1.2	0.9	0.8	2.5	1.3
1974	0.9	0.8	0.9	1.2	2.3	1.2
1979	1.2	1.2	0.9	1.3	2.8	1.5
1982	1.0	1.0	1.1	1.0	1.8	1.2
1972–82 mean	1.05	1.07	0.95	1.07	2.10	

Sediment occurred at Trenton N and S, Belleville N and S, Big Bay N, Hay Bay E, and Conway S.

Marsh substrates ranged from inorganic sediment (Conway, Belleville) to peat (Belleville, Hay Bay). Peat occurred solidly and as floating mats; detached peat islands with cattails were observed in the Trenton, Belleville, and Hay Bay areas. Where headlands or islands occur, the upsteam side is generally eroded and the downstream aggraded in both emergent and submerged vegetational zones.

Depth of transects

Depths of each transect were expressed as percentages of sampling points at 0.5-m depth intervals, which allows comparison of transects of differing length. The shallowest lines were at Trenton, Big Bay, and Hay Bay (Table 1). Belleville and Conway transects were comparable in the proportion of sampling sites at depths of less than 1 m. In the bay, rooted plants were not found below 4 m, and rarely below 3 m.

Water transparency

Mean Secchi disc measurements for late July are shown in Table 2. Light penetration values in vegetated transects were compared with values for the open water at the transect sites (Robinson 1986; Millard and Johnson 1986) and proved to be 0.1 m less. Secchi disc values at Conway differed significantly from those in the rest of the bay (Table 2). During the decade, values at Bay Bay tended to be lower than elsewhere (Table 2). The Belleville and Hay Bay transects, which had different plant cover, had similar Secchi disc values.

Values for 1979, after the start of phosphorus control, showed greater light penetration than in 1982 except in Big Bay. In 1982, divers observed similar values in Big Bay, Conway, and Belleville and noticed that the turbidity was caused by algae in Big Bay and Conway but by nonalgal organic particulates at Belleville.

Abundance of species

The relative abundance of submerged macrophytes on all transects during 1972–82 ($n = 4380$) is given below (*Myriophyllum spicatum* and *M. exalbescens* are lumped together and bryophytes, Characeae, and Lemnaceae have been omitted):

Myrophyllum spp.	26.9
Elodea canadensis	23.3
Heteranthera dubia	11.2
Najas guadalupensis	10.6
Vallisneria americana	8.2
Potamogeton pusillus	3.9
Najas flexilis	3.8
P. friesii	3.6
Ceratophyllum demersum	2.3
P. richardsonii	1.8
Ranunculus aquatilis	0.5
P. crispus	< 0.5
P. pectinatus	
Alisma gramineum	
P. zosterifolius	
P. gramineus	
Zannichellia palustris	

Plant communities and life histories

Species found on the transects are listed in Table 3, with common names. Records of previous occurrence are given in the last column.

Plants found in wetland areas but not on transects included *Potamogeton illinoensis, Sagittaria latifolia, Sparganium eurycarpum, Phragmites australis, Cyperus diandrus, Scirpus cyperinus, Nymphaea odorata*, and *Utricularia vulgaris*. All of these species had previously been found in the Hay Bay marshes by Palilionis (1977).

Transects were continued into the marshes in 1982, as far as the shrub zone which is generally waterlogged only during spring flooding. The most abundant shrubs were *Alnus rugosa, Cornus racemosa, C.stolonifera, Salix* spp., and *Spiraea alba*.

The temporal response of a community to environmental change depends partly on the longevity of its constituent species. Most of the Quinte plants were rooted perennials, amongst

TABLE 3. List of plants found on transects in 1972–82 with common names, life forms, observed overwintering forms, observed seeds or spores, and previous records of occurrence in the Bay of Quinte. Life forms: S = submerged, F = floating leaved, E = emergent; overwintering forms: U = unchanged, R = rhizome, Ro = rosette, T = turion, WB = winterbud; reproduction: Se = seeds, Sp = spores; records: M = Macoun 1883–90, P = Palilionis 1977.

	Common name	Life forms	Overwintering forms	Seeds or spores	Records
Chara braunii Gm.	Stonewort	S alga	U	Sp	
C. globularis Thuiu.	Stonewort	S alga	U	Sp	
Nitella flexilis (L.) Ag.	Stonewort	S alga	U	Sp	
Drepanocladus spp.	Moss	S moss	U	—	
Riccia fluitans L.	Liverwort	SF liverwort	U	—	
Typha latifolia L.	Cattail	E	R	Se	M, P
Najas flexilis (Willd.) Rostk. & Schmidt	Bushy pondweed	S	—	Se	M
N. guadalupensis (Spreng.) Magnus	Bushy pondweed	S	—	Se	
Potamogeton crispus L.	Pondweed	S	WB, R	Se	
P. friesii Rupr.	Pondweed	S	WB	Se	
P. pectinatus L.	Sago pondweed	S	T	Se	
P. pusillus L.	Pondweed	S	WB	Se	
P. perfoliatus L. ssp. richardsonii (Benn.) Hult.	Clasping leaf pondweed	S	R	Se	M
P. zosterifolius Schum. ssp. *zosteriformis* (Fern.) Hult.	Flat stemmed pondweed	S	R, WB	Se	M
Zannichellia palustris L.	Horned pondweed	S	R	Se	M
Alisma gramineum Gmel.	Water plantain	S, E	Ro, U	Se	
A. plantago-aquatica L.	Water plantain	S, E	Ro	Se	P
Sagittaria latifolia Willd.	Arrowhead	E	U, WB	Se	
Elodea canadensis Michx.		S	U, WB	—	
Vallisneria americana Michx.	Water celery	S	T, R	Se	M
Hydrocharis morsus-ranae L.	Frogbit	F	T	Se	
Calamagrostis canadensis (Michx.) Nutt.	Bluejoint	E	R	Se	
Phalaris arundinacea L.	Reed canary grass	E	R	Se	
Glyceria spp.	Manna grass	E	R	Se	M, P
Carex spp.	Sedge	E	R	Se	M, P
Eleocharis acicularis (L.) R. and S.	Needle rush	S, E	R	Se	
Lemna minor L.	Duckweed	F	T, U	—	
L. trisulca L.	Star duckweed	S	U	—	
Spirodela polyrhiza (L.) Schleid.	Big duckweed	F	T, U	—	
Heteranthera dubia (Jacq.) MacM.	Mud plantain	S	R	Se	M
Juncus sp.	Rush	E	R	—	M
Polygonum amphibium L.	Smartweed	F, E	R	Se	M
Ceratophyllum demersum L.	Hornwort coontail	S	T	Se	M
Nuphar variegatum Durand	Yellow water lily	F	R	Se	
Ranunculus aquatilis L.	Water crowfoot	S	U	Se	M
Cardamine pensylvanica Muhl.	Bittercress	E	—	Se	M
Callitriche hermaphroditica L.	Water starwort	S	U	Se	M
Impatiens capensis Meerb.	Jewelweed	E	—	Se	
Hypericum virginicum L.	Marsh St. John's wort	E	Ro	Se	
Epilobium sp.	Willow herb	E	—	Se	
Myriophyllum spicatum L.	Eurasian milfoil	S	U	Se	
M. exalbescens Fern.	Milfoil	S	T	Se	(?M)
Sium suave Walt.	Water parsnip	E	—	Se	
Asclepias exaltata L.	Milkweed	E	R	Se	
Cuscuta gronovii Willd.	Dodder	E	—	Se	
Lycopus americanus Muhl.	Water horehound	E	R	Se	
Scutellaria epilobiifolia Hamilton	Skull cap	E	R	—	
Utricularia intermedia Hayne	Bladderwort	S	T	Se	M
U. minor L.	Bladderwort	S	T	—	
Galium triflorum Michx.	Bedstraw	E	R	Se	
Campanula aparinoides Pursh	Marsh bluebell	E	?	Se	
Solidago sp.	Goldenrod	E	R	—	

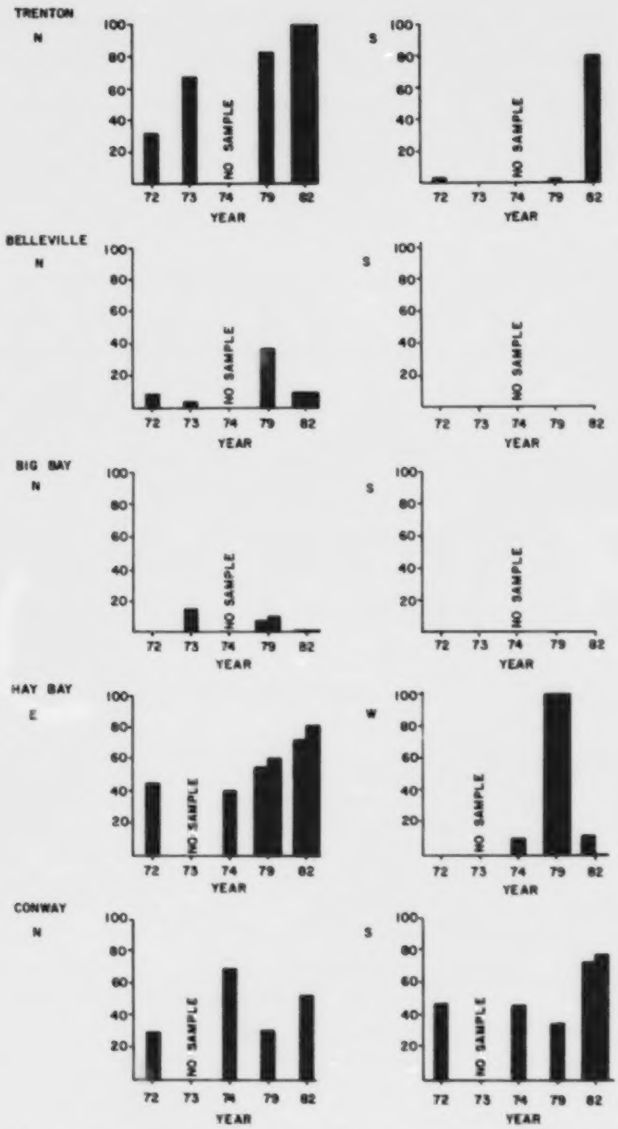

FIG. 2. Percentage cover of vegetation during 1972–82 at both ends of five transects. Missing samples are shown; other sites without histograms did not have any plant cover. For the years 1979 and 1982, cover on replicated transects is shown by contiguous histograms.

which rootless *Ceratophyllum*, duckweeds, and bryophytes drifted. Only three species had an annual turnover (*Najas flexilis* and, in the emergent zone, *Cardamine pensylvanica* and *Impatiens capensis*) (Table 3). Most species reproduced both by seeds and asexually (Table 3). The overwintering portion varied from whole plants (e.g. *Elodea*) to turions. Field observations and experiments showed that spring growth began at water temperatures of approximately 10°C; Eurasian milfoil was unique in its rapid early growth under ice in February and March (S. Painter, pers. comm.).

Reproductive stages found in the Bay were recorded as benchmark data (Table 3) because the balance between sexual and vegetative reproduction can be affected by water transparency.

In sheltered water, large weed beds were observed to persist from year to year, while on more disturbed shores the plants were destroyed by waves or ice scouring. Experimental plantings in Big Bay were uprooted by waves (Bristow et al. 1977).

Vegetation cover

The percentage of knots of which any vegetation occurred was calculated as representing cover (0–100%). In post-phosphorus control years the transects were replicated; the only site of which there was a large difference between the two lines was at Hay Bay in 1982 (Fig. 2).

The Belleville–Big Bay area had lower cover values than both the upper Bay at Trenton and the lower bay. In comparison with sites outside the Bay in 1972, cover (0–53%) was sparse; at that time it ranged from 79 to 100% in four sites in Lake Ontario (Bristow et al. 1977). The difference was not due to substrate,

TABLE 4. Percentage frequency in marsh transects 1, 2, and 2a in 1982 (2 and 2a are parallel replicates; + = < 1%; sediment type: S = silt, P = peat, PM = floating peat mat, L = limestone).

	Belleville			Hay Bay	Conway		
	1	2	2a	1	1	2	2a
Number of sampling points	87	29	29	87	58	29	29
Typha latifolia L.	82.0	55.0	58.8	79.3	84.5	58.6	58.6
Alisma plantago-aquatica Gmel.	—	—	—	—	—	13.8	13.8
Elodea canadensis Michx.	—	—	—	—	—	—	3.4
Hydrocharis morsus-ranae L.	50.6	5.0	23.5	—	—	—	—
Calamagrostis canadensis (Michx.) Nutt.	—	—	5.9	1.1	6.8	—	—
Phalaris arundinacea L.	—	—	—	—	1.7	—	—
Glyceria spp.	—	—	—	—	—	—	3.4
Carex spp.	—	—	—	3.4	—	—	—
Eleocharis acicularis (L.) R. & S.	—	—	—	3.4	—	—	—
Lemna minor L.	+	—	—	—	+	+	+
Lemna trisulca L.	+	—	—	—	—	—	—
Spirodela polyrhiza (L.) Schleid.	—	—	—	+	—	—	—
Heteranthera dubia (Jacq.) MacM.	—	—	—	—	3.4	—	—
Juncus sp.	—	—	—	1.1	—	—	—
Polygonum sp.	—	—	—	—	—	—	3.4
Ceratophyllum demersum L.	—	—	—	—	—	3.4	3.4
Cardamine pensylvanica Muhl.	—	—	—	—	6.9	—	—
Callitriche hermaphroditica L.	—	—	—	—	2.3	—	—
Impatiens capensis Meerb.	—	15.0	23.5	3.4	3.5	6.9	10.3
Hypericum virginicus L.	—	—	—	5.7	—	—	—
Epilobium sp.	—	5.0	—	2.3	—	—	—
Sium suave Walt.	—	—	—	2.3	—	—	—
Asclepius exaltata L.	—	—	—	1.1	—	—	—
Cuscuta gronovii Willd.	2.3	—	—	—	—	—	—
Lycopus americanus Muhl.	2.3	—	—	5.7	—	—	—
Scutellaria epilobiifolia Hamilton	—	10.0	—	—	—	—	—
Utricularia intermedia Hayne	—	—	—	3.4	—	—	—
Utricularia minor L.	—	—	—	1.1	—	—	—
Galium triflorum Michx.	—	5.0	—	3.5	—	—	—
Campanula aparinoides Pursh.	—	—	—	10.3	5.2	—	—
Solidago sp.	—	—	—	—	1.7	—	—
Riccia fluitans L.	+	—	—	+	—	+	+
Musci	+	—	+	+	+	+	+
Sediment type	P	S, L	S, L	PM	P	S	S

which was similar to the limestone sites within the Bay. Highest cover was found in sedimented areas; however, on the Trenton transect in 1982, plants grew on bare limestone but not on the sediment at the same depth.

Lumping together pre-phosphorus control years and post-phosphorus control years, cover values increased ($\bar{x}$ for 1972–74 = 22.0 ± 20.4; $\bar{x}$ for 1979–81 = 58.9 ± 68.4), but the difference in means was not significant at the 0.05 level because of the high variance ($t = 0.098$). While no overall temporal improvement occurred, the values in Belleville, Big Bay, and Hay Bay E were greater in 1979 than in 1982.

The highest precontrol values were at Trenton N and Conway N. Postcontrol values, which ranged from 0 to 100%, were highest at Trenton N and Hay Bay.

In an attempt to explain the lower cover found in the Belleville and Big Bay area, a predicted cover value was calculated for each transect using two possible values for the depth of the euphotic zone, and the known depth of the transect (Table 1). The values used for the calculations were euphotic zones of 2 or 4 m; these values approximated the water transparency found in the upper bay and at Conway, respectively, during the decade (cf. Table 2). The predicted cover values (percentages) given below are for July, and assume that water transparency is the only factor controlling depth distribution of macrophytes.

Transect	Assumed depth of euphotic zone	
	2 m	4 m
Trenton	71	96
Belleville	28	83
Big Bay	60	95
Hay Bay	60	96
Conway	31	82

Comparison of actual cover (Fig. 2) with above values showed that all transects except Big Bay reached predicted cover for a zone of 2 m or more during 1979–82. The main factor limiting growth in the Belleville–Big Bay area is therefore not the morphometry of the basin in these areas. The predicted cover values also indicate that differences between transects should be more marked with a shallow euphotic zone (range with 2 m = 43%, with 4 m = 14%).

Cover in the marsh vegetation was estimated by intercepts

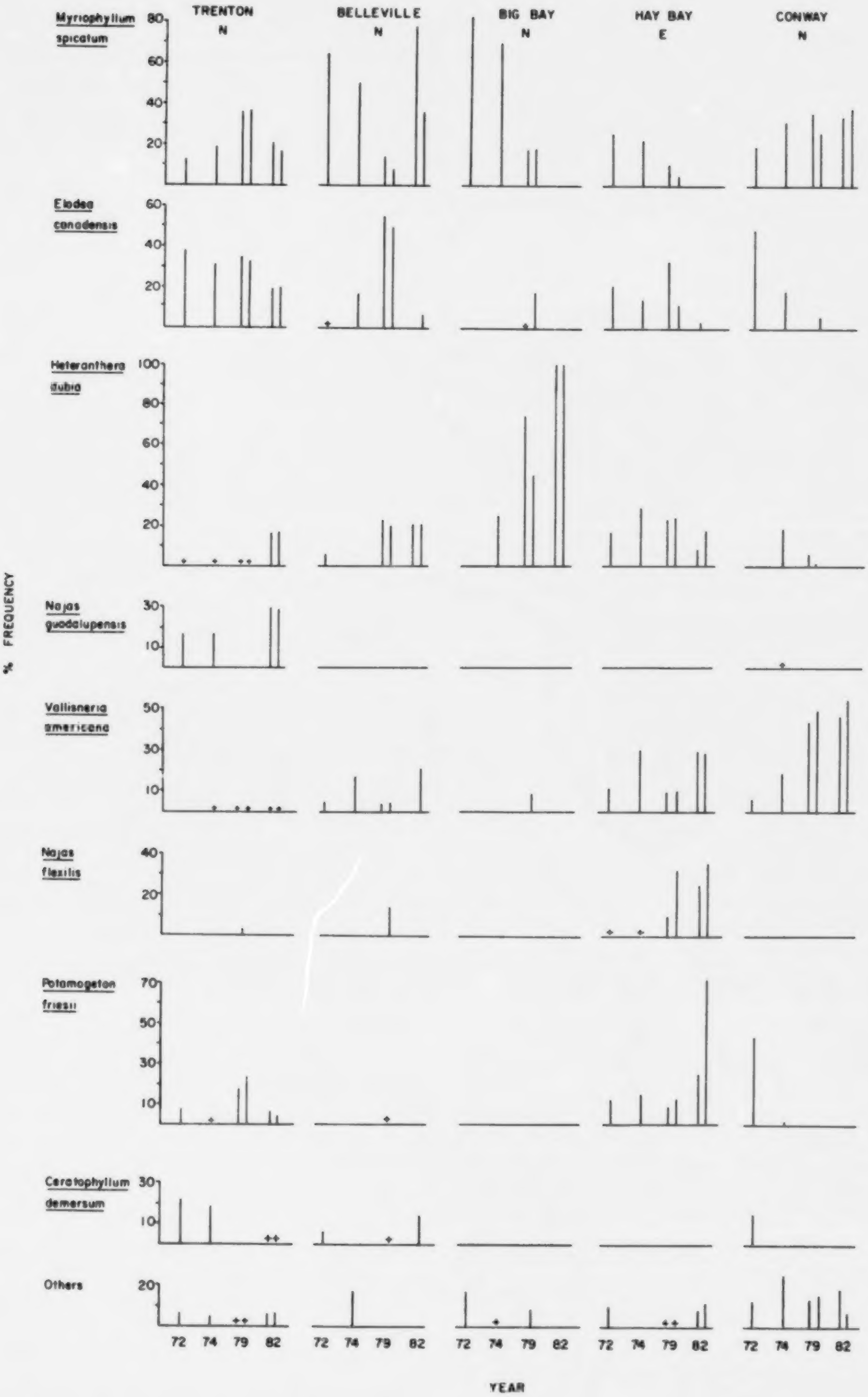

FIG. 3. Percentage frequency of eight abundant species at one end of five transects during the period 1972–82. Less than 2% frequency is shown by a plus sign.

along transects in the usual method for terrestrial transects and can exceed 100% where there is more than one layer of vegetation (Smith 1980). The range of values in 1982 was 86–144%.

Dominant plants: intersite and interyear differences

Relative abundance data showed the dominant plants to be *Myriophyllum spicatum*, *Elodea canadensis*, *Heteranthera dubia*, *Najas guadalupensis*, and *Vallisneria americana*. The percentage frequency of these dominants, together with *Potamogeton friessii* and *Ceratophyllum demersum*, was calculated for vegetated transect points for four years, 1972, 1974, 1979, and 1982 (Fig. 3). Percentage frequency in 1982 was calculated for emergent vegetation (Table 4).

Myriophyllum spicatum was found in all years at Trenton N, Belleville N, and Conway N and in the other transects except in 1982. We have followed Aiken (Aiken et al. 1979; Aiken 1981) in retaining species status for both the Eurasian *M. spicatum* L. and the native *M. exalbescens* Fern. Both species were present in 1971, but were not differentiated in our field data until 1975. *Myriophyllum spicatum* is an introduced species which spread widely in North America during the 1960s and 1970s (Aiken et al. 1979; Carpenter 1980). Its populations generally peak in 5–10 yr. Its occurrence at the Bay transects during 1972–82 was as follows:

	1972	1982	1979	1982
Percentage of samples with Eurasian milfoil	6.47	9.2	10.8	10.1
Number of samples	896	523	1148	1344

In Hay Bay, Big Bay, and Trenton it has become less frequent (Fig. 3), but in Belleville (and in Picton Harbour) it has increased in the 1980s. Its distribution did not appear to be related to sediment type.

As might be expected of perennial rooted plants, species tended to persist during the decade at particular sites; for example, *Najas guadalupensis* was present in 1972, 1974, 1979, and 1982 at Trenton N, but did not occur at all on the Belleville N, Big Bay N, and Hay Bay E transects (Fig. 3).

In the Trenton, Hay Bay, and Conway transects, year-to-year fluctuations in the frequency of dominant species were less extreme than in Belleville and Big Bay. The frequency values should be considered in relation to cover (Fig. 2); the marked fluctuations in annual frequency of *Heteranthera* at Big Bay and of *Myriophyllum* and *Elodea* at Belleville occurred in transects with very little cover. *Myriophyllum spicatum* and *Heteranthera dubia* were dominant where the community was most stressed.

None of the dominants showed a consistent temporal trend in frequency at all transects.

In the emergent vegetation, in 1982, cattail (*Typha latifolia*) was dominant at Belleville, Hay Bay, and Conway (Table 4). *Impatiens capensis*, an annual generally occupying patches of mud between the cattails, was also present in all three sites. At Belleville, an invasive species (frogbit, *Hydrocharis morsus-ranae*) had a high frequency in one transect. The spread of this species in North America since 1939 has been recorded by Dore (1954, 1968); in Europe, it occurs in silted backwaters or mesotrophic peat dykes (Haslam 1978).

Diversity

Two measures of diversity were used to compare transects, species richness (*S*) and the Shannon–Wiener index (*H'*). *S* is the number of species per sampling unit or area and contains no information on the evenness component of the community and it is useful for water plants because of their indeterminate growth and the difficulty of distinguishing individual plants:

S (number of species per 116 transect points)

Submerged transects	1972	1973	1974	1979(2)	1982(2)	Mean
Trenton N.	8	11	—	8, 6	9, 8	8.3
Belleville N.	5	4	—	5, 6	2, 5	4.5
Big Bay N.	2	3	—	3	1, 1	2.0
Hay Bay E.	11	—	6	8, 7	6, 6	7.3
Conway N.	8	—	10	5, 7	5, 3	6.3
Marsh transects						
Belleville 1					8	
Belleville 2 and 2a					6, 5	
Hay Bay					18	
Conway 1					11	
Conway 2 and 2a					10, 7	

The bay showed three subdivisions in regard to species richness. West of Trenton it was high; during the decade, 16 species were found on the Trenton transect, although not more than 11 in one year. McCombie (1967) showed that, in the 1960s, the head of the Bay was not as eutrophic as the rest of the area. In the Belleville–Big Bay area, *S* was very low, as was cover. In the lower bay, *S* was not so high as at Trenton and showed a decline during the decade; the total number of submerged species found on the Conway transects was 11. Comparing mean values for 1972–74 with those from 1979–82, there was a nonsignificant change from 6.8 to 6.3.

In wetland transects, species richness was greater in Hay Bay (20 species, including mosses) than in Belleville (8) or Conway (11). The Belleville marsh transect showed the same property as the underwater transects in that area. Species richness was presumably lower because of the dominance of frogbit and milfoil on these transects.

The Shannon–Wiener index (*H'*) was used to calculate diversities for two inshore lengths of transect at each site (Table 5). The most diverse site in a single year was Trenton N, and the least diverse site (excluding the Big Bay and Belleville transects which had insufficient plants for calculation of *H'*) was Trenton S.

Values of *H'* and distance offshore for selected transects are shown graphically in Fig. 4. While the same type of pattern was evident in 1972 and 1982 in Hay Bay E and Conway N, this was not so at Trenton N. In most of the transects the highest *H'* value tended to occur offshore. A possible explanation may be that the immediate shoreline is disturbed or stressed by waves and ice, reducing diversity. In Hay Bay and Conway the diversity diminished towards the offshore end of the transects, as deeper water was reached.

Similarity coefficients

Different years and different transects were compared, using the Jaccard coefficient S_j (Table 6). Interyear similarity was low at all sites. Within-year similarity between the ends of transects was low, with the exception of Big Bay N and S in 1979 (which had low species richness).

High similarity was found between the following sites: Hay Bay W 1979 and Big Bay N 1979, Conway N 1982 and Conway S 1979, Conway S 1979 and Trenton N 1982. These pairs of transects were all in post-phosphorus control years. They were not matched in cover or diversity (*H'*).

The Jaccard coefficient values can be interpreted to mean that all the transects belonged to one community type which had

TABLE 5. Diversity (H') on transects (58 m in length) starting at 0.5 m in depth and running offshore. Lemnaceae, bryophytes, and Characeae are omitted.

Year	Conway S	Conway N	Hay Bay E	Hay Bay W	Big Bay S	Big Bay N	Belleville S	Belleville N	Trenton S	Trenton N
1972	1.254	1.011	1.851	—	No plants	No plants	No plants	1.314	0.000	1.413
1974	0.839	1.552	1.443	—	No plants	0.736	No plants	0.693	No plants	1.872
1979A	0.808	0.773	1.499	1.052	0.575	0.703	No plants	1.553	0.000	1.631
1979B	—	—	1.360	1.039	0.917	0.956	—	—	—	—
1982A	0.929	1.113	1.482	1.181	—	0.000	No plants	0.540	0.901	0.876
1982B	0.935	1.151	1.328	0.960	—	0.000	—	1.342	0.693	—

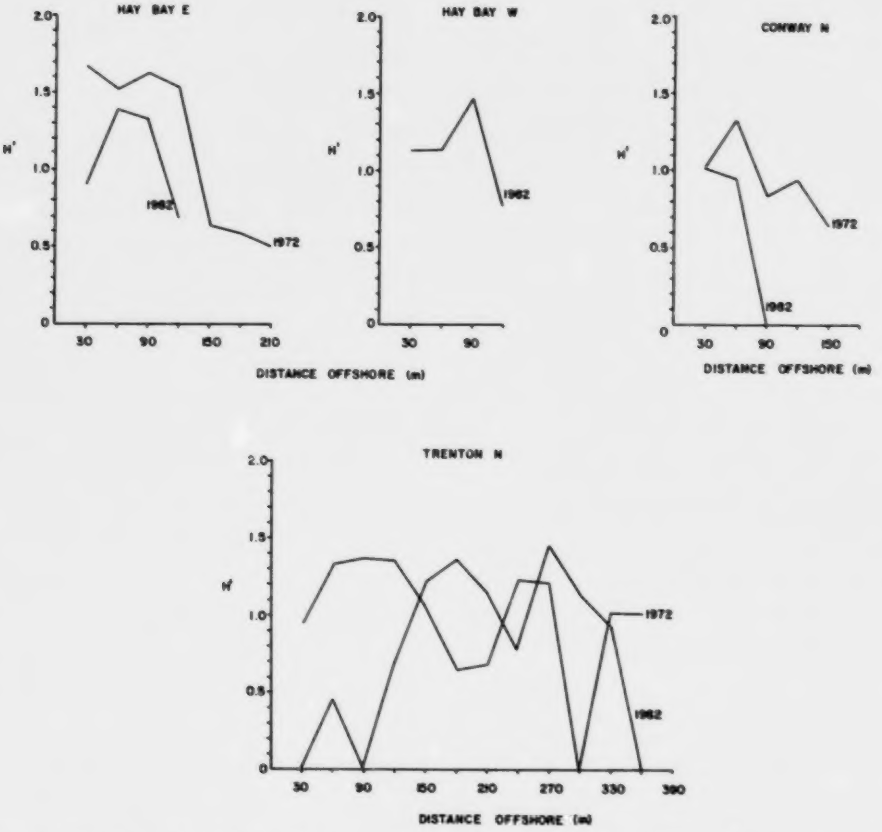

FIG. 4. Diversity (H') of the plant community and distance offshore at Hay Bay, Conway N, and Trenton N.

high variance from place to place and year to year. Patchiness of the vegetational mosaic was also evident from replicated transects, for example in the variation in frequency of *Myriophyllum spicatum* at Belleville (Fig. 3).

Standing Crop, Plant Plasticity, and Phosphate Content

Methods

Sampling submerged macrophytes

To measure standing crop, samples of submerged vegetation were collected into a plastic bag by a diver from an area of 25 × 25 cm. Sites (20 per annum) were randomly chosen from a grid covering the Bay, which resulted in a large number of fruitless dives; in 1979 and 1982 the grid was therefore confined to the euphotic zone. Plants were washed and ovendried using the method of Craig (1976). Each sample was dried at 150°C in a forced draught oven to constant weight (usually 48 h). Samples were collected in a desiccator before weighing. Subsamples used to determine ash weight were placed in a muffle furnace at 550°C for 30 min, cooled in a desiccator, and weighed.

Emergent plants for standing crop measurement were collected along transects (see Macrophytes from 1972 to 1982, Methods).

To estimate possible changes in plant form as water clarity changed, stem length of *Elodea canadensis* was measured using 10 randomly collected specimens from each transect at 1 m depth. For phosphate analysis, chopped roots and shoots were mixed together (for submerged plants, the mixture from biomass samples were used; for emergents only *Typha latifolia* was

TABLE 6. Jaccard similiarity coefficients (S_j) within and between ends of transects during 1972, 1974, 1979, 1982. The most similar communities have a coefficient of 0.750. HB = Hay Bay, C = Conway, BB = Big Bay, B = Belleville, T = Trenton.

	HB E 72	HB E 74	HB E 79	HB E 82	HB W 79	HB W 82	C S 72	C S 74	C S 79	C S 82	C N 72	C N 74	C N 79	C N 82	BB N 74	BB N 79	BB N 82	BB S 72	B N 72	B N 74	B N 79	B N 82	T S 72	T S 82	T N 72	T N 74	T N 79	T N 82
HB E 72		0.384	0.33	0.286	0.181	0.231	0.333	0.273	0.154	0.231	0.333	0.286	0.273	0.167	0.273	0.182	0.091	0.250	0.333	0.182	0.308	0.083	0.091	0.154	0.231	0.538	0.308	0.167
HB E 74			0.556	0.500	0.500	0.375	0.333	0.500	0.250	0.333	0.375	0.444	0.286	0.286	0.125	0.286	0.167	0.429	0.571	0.333	0.625	0.143	0.167	0.250	0.222	0.364	0.500	0.286
HB E 79				0.454	0.500	0.625	0.182	0.250	0.375	0.455	0.300	0.250	0.375	0.222	0	0.333	0.111	0.444	0.273	0.222	0.600	0.222	0.111	0.250	0.167	0.308	0.500	0.333
HB E 82					0.286	0.375	0.200	0.125	0.250	0.333	0.272	0.300	0.250	0.286	0	0.111	0.143	0.222	0.200	0.286	0.400	0	0.143	0.375	0.222	0.214	0.300	0.111
HB W 79						0.286	0.111	0.167	0.333	0.429	0.186	0.222	0.167	0.167	0	0.750	0.250	0.600	0.286	0.200	0.571	0.500	0	0.333	0.286	0.167	0.667	0.400
HB W 82							0.100	0.143	0.286	0.333	0.260	0.200	0.167	0.143	0	0.167	0.200	0.500	0.250	0.400	0.500	0.167	0.200	0.500	0.111	0.154	0.429	0.333
C S 72								0.500	0.429	0.333	0.375	0.300	0.286	0.500	0.250	0.111	0	0.222	0.500	0.125	0.273	0.125	0.143	0.100	0.200	0.309	0.182	0.250
C S 74									0.400	0.400	0.333	0.429	0.500	0.500	0.200	0.200	0	0.400	0.600	0.250	0.250	0.250	0.333	0	0.143	0.300	0.286	0.500
C S 79										0.167	0.286	0.222	0.400	0.750	0	0.400	0	0.600	0.286	0.200	0.375	0.500	0.200	0.333	0.125	0.167	0.429	0.750
C S 82											0.222	0.222	0.286	0.500	0	0.286	0	0.429	0.222	0.143	0.444	0.333	0.167	0.250	0.100	0.143	0.500	0.500
C N 72												0.333	0.333	0.333	0	0.286	0.167	0.429	0.571	0.333	0.444	0.143	0.167	0.111	0.571	0.455	0.500	0.286
C N 74													0.250	0.250	0.100	0.222	0.125	0.333	0.444	0.250	0.273	0.111	0.125	0.091	0.300	0.385	0.273	0.222
C N 79														0.500	0	0.200	0	0.400	0.333	0.250	0.250	0.250	0.333	0	0.143	0.182	0.286	0.500
C N 82															0	0.167	0	0.333	0.286	0.200	0.222	0.200	0.250	0.143	0.125	0.167	0.250	0.400
BB N 74																0	0	0	0.143	0	0	0	0	0	0	0.182	0	0
BB N 79																	0.333	0.750	0.333	0.250	0.429	0.667	0	0.400	0.333	0.182	0.500	0.500
BB N 82																		0.250	0.200	0.500	0.167	0	0	0.250	0.200	0.100	0.167	0
BB S 79																			0.500	0.500	0.571	0.500	0.250	0.333	0.500	0.173	0.667	0.750
B N 72																				0.400	0.500	0.167	0.200	0.125	0.429	0.500	0.375	0.333
B N 74																					0.286	0	0.500	0.200	0.200	0.200	0.333	0.250
B N 79																						0.286	0.143	0.375	0.333	0.308	0.625	0.429
B N 82																							0	0.200	0.67	0.091	0.333	0.667
T S 72																								0	0	0.100	0.167	0.667
T S 82																									0.125	0.77	0.250	0.167
T N 72																										0.500	0.375	0.143
T N 74																											0.333	0.182
T N 79																												0.500
T N 82																												

used). Samples from 10 sites were mixed together. Total phosphate was analysed after extraction of air-dried ground material with sulphuric acid and potassium persulphate; in 1979, analysis was done by the Ontario Ministry of the Environment.

Area of submerged and emergent macrophytes

An aerial survey was flowen by the Ontario Centre for Remote Sensing at the time of maximal biomass in late July 1979. Colour prints were made from a series of 18 flight lines varying from 0.5 to 18 km in length. In these prints it was possible to distinguish three types of emergent vegetation and two of submerged or floating-leaved plants. Ground truth for the zones was gathered in the field in 1979 and was also based on previous field work.

The vegetational zones were transferred to a 1 : 50 000 map (Ontario 31 C/3 and C/4). At this scale it was impossible to work with more than two categories, and the zones were accordingly lumped as (1) floating-leaved and submerged vegetation and (2) emergent reed beds, dominated by *Typha latifolia*, including grass-dominated areas and excluding shrubby areas.

Three problems were encountered in transferring the information to the map. (1) Shorelines in photographs and on the map did not coincide because of changes in water level, drainage, building of jetties, etc. This was corrected by using charts and detailed maps of areas such as Carrying Place. (2) The flight line was aligned in such a way that the upper portions of marshes were omitted. Contour lines were used to extrapolate the level of the shrub zone through these marshes, which were visited to determine their floristic composition. The most considerable areas not included in the aerial survey were approximately 1500 ha of wetland west of Muscote Bay and in the upper part of Marysville Creek marsh. (3) Rippling and cloud reflection distorted the image of submerged weed beds in some areas so that it was not possible to find their offshore limits. In these areas the bottom level of the euphotic zone was drawn onto the navigational chart and was assumed to be the offshore limit for plants.

Area of plant cover was underestimated in all areas where the photographs were unclear.

The plant zones were traced, the tracings were transferred onto a computer, and the areas were calculated in square metres.

Results

Measures of standing crops

Standing crop (organic weight) was measured at randomly chosen points and the number of sample sites that contained plants was small ($n = 55$). The overall mean for 1972, 1973, 1979, and 1982 was 26.12 g · m^{-2}. Annual means and ranges were as follows:

	Number of samples	Mean (g · m^{-2})	Range
1972	5	37.2	0.1–111.0
1973	14	20.3	0.1–145
1979	17	35.1	6.0–116.0
1982	19	18.7	7.0–86.0

Using Tukey's and Duncan's multiple range tests, no two pairs of means were significantly different.

In wetland transects, *Typha latifolia* occurred with a frequency of 55–86% and was much the largest plant. For these transects, only cattails were used in measuring standing crop, which had a mean of 1.5 km · $^{-2}$ in 1979. This value was typical for cattails (Taylor and Crowder 1983).

Plant plasticity

It was anticipated that reduced algal density might change macrophyte growth, resulting in significant differences in plant form. *Elodea canadensis* was chosen as a representative dominant and native species. Mean values for stem lengths (centimetres) of 10 randomly collected plants from the same depth on each transect, for years before and after phosphorus control, were calculated:

Transect	1972	1979
Trenton	54.67	44.88
Belleville	33.00	30.25
Big Bay	—	22.75
Hay Bay	31.29	48.00
Conway	24.50	48.00

Although there was a trend for high values to occur in Trenton and Hay Bay, there were no significant differences between means for sites or years because of high variance.

Estimation of area and phosphate content of submerged and emergent plant

From 1979 photographs, the area of submerged and floating-leaved macrophytes was calculated to be 6 272 000 m^2 (627 ha) and the area of the cattail community 2 824 000 m^2 (2824 ha). An additional 1250 ha of cattails west of Muscote Bay and in Marysville Creek Marsh, in places which had not been covered by the flight lines, was estimated from the 1982 topographic map and field information. Total marshland was therefore estimated at 4074 ha.

Mean standing crop of the submerged zone was calculated as 28 g · m^{-2} in 1979. Boyd's value of 0.28% (Boyd 1970) phosphate was used to estimate the phosphate content of submerged vegetation as 494 kg P (0.49 t).

Phosphate content of the cattail plants from three transects averaged 1.47 mg P · g^{-1} (range 0.77–1.78). Comparable values for phosphorus content of cattails have been given by Boyd (1970), Klopatek (1978), Dykyjova and Ulehlova (1978), and Van der Valk and Davis (1978). The standing crop in the emergent zone was estimated at 1.5 km · m^{-2} (cf. Whigham et al. 1978; Taylor and Crowder 1983). The content of total phosphorus in the standing crop of 4074 ha of wetlands was calculated to be 89891.7 km (89.89 t).

Discussion

The community of macrophytes in the Bay of Quinte lost some species between the 1880s and 1950s. During the rapid eutrophication of the 1950s and early 1960s, its biomass and area increased, but by 1972 much of the submerged zone had become sparsely vegetated. During 1972, plants grew to a depth of only 2 m, except at Conway where the bottom limit was 4 m.

Percentage cover on transects had a mean value of 22% during 1972–82, which was low in comparison with similarly sampled areas in Lake Ontario (Wolfe Island and Simcoe Island, 75%) and in mesotrophic lakes in the region (100%) (Crowder et al. 1977a). In the postcontrol period, cover increased, but not significantly because of high variance. An increase in 1979 at Belleville and Big Bay was followed by a decrease in 1982. Standing crop (mean value 26 g · m^{-2}) was also low throughout the decade; a comparative value from a mesotrophic lake in the region (Lake Opinicon) was 248 $g \cdot m^{-2}$. Variance was high, but this is usual in macrophytic communities; LeCren and McConnell (1980) reported a range of 1–1154 $g \cdot m^{-2}$ in the literature. Stem length in *Elodea* showed no difference in pre- and post-control years; lengths ranged from 22 to 55 cm, and plants from Wolfe Island had a mean of 32 cm.

Species richness (S) in submerged areas was low in comparison with mesotrophic lakes in the region (Crowder et al. 1977a, 1977b). No general improvement in species richness or diversity (H') occurred after phosphorus control and, indeed, in Hay Bay richness decreased. Species richness of emergent areas (ranging from 5 at Belleville to 18 at Hay Bay) was lower than in comparable marshes in the region e.g. Lake Opinicon, 22; Wiltse Marsh, 26).

While individual species tended to persist on particular transects, a comparison of cover, biomass, relative frequency, species richness, and diversity showed that weed beds were not homogeneous and that species groupings were not stable from year to year. The Jaccard coefficient of similarity (S_j)) indicated some increase in similarity between transects after phosphorus control, for example, between Trenton and Conway. Trenton and Hay Bay were most alike in cover values, and Robinson's cluster analysis of chemical data showed that these two sites clustered together at the first level, using either chlorophyll *a* or nitrogen as a criterion (Robinson 1986). Belleville and Hay Bay were notable for barrenness and low diversity throughout the study; this part of the Bay has the longest history of eutrophication and pollution (Mudroch and Capobianco 1980; Sly 1986).

The five underwater transects were chosen by Project Quinte, but appeared to give a representative view of the Bay, except for the omission of an area of lush vegetation near Forrester's Island. The time and cost of diving, essential for sampling the bottom flora in such murky water, were limiting factors. The technique used established *Najas guadalupensis*, previously considered rare in eastern Ontario, as a common species. Because transects were started at a depth of 0.5 m, the floating-leaved plants were underrepresented, in shallow backwaters, the number of species were often observed to be high.

During the decade, the dominant plants were *Myriophyllum spicatum*, *Heteranthera dubia*, *Najas guadalupensis*, and *Vallisneria americana*. These species occur in eutrophic sites in Ontario (Crowder et al. 1977a; Miller 1979) and elsewhere (Mickle 1977; Best 1982). The contemporaneous development of eutrophication and invasion by Eurasian milfoil has been observed in many other sites such as Chesapeake Bay and the Finger Lakes (Oglesby 1978). *Myriophyllum spicatum* tolerates both turbidity and pollution (Oglesby 1978; Adams and McCracken 1974; LeCren and McConnell 1980; Kimbel 1982) and begins growth in the Bay of Quinte earlier in spring than its competitors. As the milfoil increases, there is generally a decrease in diversity, and particularly a loss of species of *Potamogeton* (Nichols and Mori 1971; Bloomfield 1978). Three species of *Potamogeton* growing at Belleville a century ago (*P. gramineus*, *P. perfoliatus*, and *P. zosterifolius*) were not found in 1972–82, and only 6 species occurred on transects in comparison with 11 species in comparable samples from local mesotrophic lakes (Crowder et al. 1977a, 1977b). On a small scale, the same phenomenon was found in the emergent vegetation at Belleville, where frogbit (*Hydrocharis morsus-ranae*), another introduced aquatic weed, was found with low diversity. *Typha latifolia* dominated the emergent marshes, as on many Lake Ontario shorelines (Sparling 1979; Pringle 1980; Mudroch 1981; Maltby 1982; Environment Canada and Ontario Ministry of Natural Resources 1984).

Increasing nutrient levels presumably caused the increase in weed beds reported during the 1950s and early 1960s. When a hypereutrophic state was reached, decreased transparency of the water column, due to algal biomass, suppressed the macrophytes. In 1979, only 14% of the area of the Bay was occupied by submerged plants, which did not grow below a depth of 2 m, except at Conway. At Conway the vegetated zone was 4 m in depth; had similar light conditions prevailed throughout the middle and upper Bay, 40% of its area could have been occupied by macrophytes. This estimate, based on morphometry, should perhaps realistically be reduced to 30% to allow for shores exposed to waves or ice scouring (Forest et al. 1978; Keddy 1983). Water transparency has increased as algal biomass has diminished during the post-phosphorus control period (Robinson 1986; Millard and Johnson 1986), so that the macrophytes might have been expected to recover. In our transects in the shallows, however, the expected increase in water transparency was not found, presumably because of suspended sediment. The macrophytes have not, therefore, been able to recolonize their former habitats in deeper water.

Anomalies found in the macrophyte data, such as higher cover in 1979 than in 1982 at Belleville and Big Bay, were found in other data sets. In 1982, phosphorus loading was higher than in 1979 at Trenton, Belleville, and Napanee (Owen 1983), and Robinson (1986) has pointed out that sewage plants do not maintain a uniform efficiency. Another anomaly was decreased species richness occurring in Hay Bay. Here, chlorophyll *a* has in fact increased, cutting out the light available for macrophytes; point sources are not the problem in Hay Bay, but increased agricultural runoff of phosphorus (Bynoe 1979; Percival 1979). The macrophytes appear to be very sensitive indicators of water quality, as Forest et al. (1978) have pointed out: "critical indicators of eutrophication are clarity of water and depth of rooted vegetation."

In 1979 it was conservatively estimated that the phosphate content of the standing crop of submerged weed beds was 0.49 t and that of the emergent wetlands 89.89 t. The observed overwintering state of the plants suggests that most of the submerged biomass is turned over annually. In the wetlands, however, the phosphorus is largely sequestered in rhizomes. Some areas of the wetlands are accumulating peat, but the peat and cattails can break off as islands, carrying their phosphate content out to Lake Ontario.

While there is a considerable literature on the effects of increasing eutrophication on macrophytes, the data presented here are unusual in recording the early stage of phosphorus control. The community has not made any rapid recovery, although there has been a trend towards increased cover. Its diversity remains low, partly because the Eurasian milfoil invasion has not yet declined, partly perhaps because there was a loss of sediment and propagules during the hypereutrophic phase.

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References

Adams, M. S., and M. D. McCracken. 1974. Seasonal production of the *Myriophyllum* component of the littoral of L. Wingra, Wisconsin. J. Ecol. 62: 457–467.

Aiken, S. G. 1981. A conspectus of *Myriophyllum* (Haloragaceae) in North America. Brittonia 33(1): 57–69.

Aiken, S. G., P. R. Newroth, and I. Wile. 1979. The biology of Canadian weeds. 34. *Myriophyllum spicatum* L. Can. J. Plant Sci. 59: 201–215.

Bannister, T. T. and R. C. Bubeck. 1978. Limnology of Irondequoit Bay, Munroe County, New York, p. 106–223. *In* J. A. Bloomfield [ed.] Lakes of New York State. Vol. II. Ecology of the lakes of western New York. Academic Press, New York, NY.

Best, E. P. 1982. The aquatic macrophytes of L. Vechten. Species composition, spatial distribution and productivity. Hydrobiologia 95: 65–77.

Bloomfield, J. A. [ed.] 1978. The lakes of New York State. Vol. 1. Ecology of the Finger Lakes. Academic Press, New York, NY.

Boyd, C. E. 1970. Chemical composition of wetland plants, p. 155–168. *In* G. E. Good, D. F. Whigham, and R. I. Simpson [ed.] Freshwater wetlands: ecological processes and management potential. Academic Press, New York, NY.

Bristow, J. M., A. A. Crowder, M. R. King, and S. VanderKloet. 1977. The growth of aquatic macrophytes in the Bay of Quinte prior to phosphate removal by tertiary sewage treatment (1975–1976). Naturaliste Can. 104: 465–473.

Bynoe, M. C. 1979. Spatial and temporal trends in the fluvial transport of sediment-associated heavy metals in Wilton Creek, S.E. Ontario. M.Sc. thesis, Queen's University, Kingston, Ont.

Canadian Hydrographic Service. Great Lakes Pilot. Vol. 1. 1957, 1963, 1968 and 1975. Department of Energy, Mines and Resources, Ottawa, Ont.

Carpenter, S. R. 1980. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. Can. J. Bot. 58(5): 527–535.

Craig, S. 1976. Seasonal development of structure in two macrophytic communities in L. Opinicon, Ontario. M.Sc. thesis, Queen's University, Kingston, 104 p.

Crowder, A. A., J. M. Bristow, M. R. King, and S. VanderKloet. 1977a. The aquatic macrophytes of some lakes in southeastern Ontario. Naturaliste Can. 104: 457–464.

1977b. Distribution, seasonality and biomass of aquatic macrophytes in L. Opinicon (eastern Ontario). Naturaliste Can. 104: 441–456.

Dore, W. G. 1954. Frogbit (*Hydrocharis morsus-ranae* L.) in the Ottawa River. Can Field-Nat. 68: 180–181.

1968. Progress of the European frog-bit in Canada. Can. Field-Nat. 82: 76–84.

Dykyjova, D., and B. Ulehlova. 1978. Structure and chemistry of the fishpond bottom. *In* D. Dykyjova and J. Kvet [ed.] Pond littoral ecosystems. Springer Verlag, New York, NY.

Eaton, S. W., and L. P. Kardos. 1978. The limnology of Canandaigua Lake, p. 226–312. *In* J.A. Bloomfield [ed.] Lakes of New York State. Vol. 1. Ecology of the Finger Lakes. Academic Press, New York, NY.

Environment Canada and Ontario Ministry of Natural Resources. 1984. An evaluation system for wetlands of Ontario south of the Precambrian Shield. Canadian Wildlife Service, Ottawa, Ont.

Forest, H. S., J. Q. Wade, and T. F. Maxwell. 1978. The limnology of Conesus Lake, p. 122–225. *In* J. A. Bloomfield [ed.] Lakes of New York State. Vol. 1. Ecology of the Finger Lakes. Academic Press, New York, NY.

Haslam, S. M. 1978. River plants. Cambridge University Press, Cambridge. 396 p.

Jupp, B. P., and D. H. N. Spence. 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. I. Effects of phytoplankton. J. Ecol. 65: 175–186.

Keddy, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology 64(2): 331–344.

Kimbel, J. C. 1982. Factors influencing potential intralake colonization by *Myriophyllum spicatum* L. Aquat. Bot. 14: 295–307.

Klopatek, J. M. 1978. Nutrient dynamics of fresh water riverine marshes and the role of emergent macrophytes, p. 195–242. *In* G. E. Good, D. F. Whigham, and R. I. Simpson [ed.] Freshwater wetlands: ecological processes and management potential. Academic Press, New York, NY.

LeCren, E. D., and R. H. L. McConnell [ed.] 1980. The functioning of freshwater ecosystems. Cambridge University Press, Cambridge. 588 p.

Macoun, J. 1878. Catalogue of the phaenogamous and cryptogamous plants (including lichens) of the Dominion of Canada south of the Arctic Circle. F.W. Hynes, Belleville, Ont.

1883–90. Catalogue of Canadian plants. Parts 1–5. Gen. Surv. of Canada, Ottawa, Ont.

Maltby, L. 1982. Draft for an evaluation system for wetlands of Ontario, south of the pre-Cambrian shield. Canadian Wildlife Service and Ontario Ministry of Natural Resources, Ottawa, Ont.

McCombie, A. M. 1967. Some physical and chemical characteristics of the Bay of Quinte. Res. Rep. Ont. Dep. Lands For. 79: 1–56.

McNaughton, S. J., and L. L. Wolf. 1979. General ecology. Holt, Rinehart & Winston, New York, NY. 710 p.

Mickle, M. 1975. The comparative mineral nutrition of nuisance aquatic plants. Ph.D. thesis, University of Wisconsin, Madison, WI.

Millard, E. S., and M. G. Johnson. 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Miller, G. E. 1979. A classification of Ontario lakes based on their submersed and floating macrophyte flora. M.Sc. thesis, University of Guelph, Guelph, Ont.

Mudroch, A. 1981. A study of selected Great Lakes coastal marshes. Environment Canada, National Water Research Institute, Inland Waters Directorate, Sci. Publ. Ser. No. 122, Burlington, Ont.

Mudroch, A., and J. A. Capobianco. 1980. Impact of mining activities on aquatic sediments in the Moira River Basin, Ontario. J. Great Lakes Res. 6(2): 121–128.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nichols, S. A., and S. Mori. 1971. The littoral macrophyte vegetation of L. Wingra: an example of a *Myriophyllum spicatum* invasion in a southern Wisconsin Lake. Trans. Wisc. Acad. Sci. Arts Lett. 59: 107–119.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences. 2nd ed. McGraw-Hill, Toronto, Ont.

Oglesby, R. T. 1978. The limnology of Cayuga Lake, p. 2–121. *In* J. A. Bloomfield [ed.] Lakes of New York State. Vol. 1. Ecology of the Finger Lakes. Academic Press, New York, NY.

Owen, G. 1983. Annual report of Project Quinte. Ontario Ministry of the Environment, Kingston, Ont.

Palilionis, A. 1977. A study of Big Island, Hay Bay and Rideau Marsh in relation to marsh management. Ontario Ministry of Natural Resources, Toronto, Ont.

Percival, J. 1979. The spatial and temporal flux of sediment related phosphorus, clay mineralogy and soluble anions in Wilton Creek, S.E. Ontario. M.Sc. thesis, Queen's University, Kingston, Ont.

Peters, W. A. 1951. Feathers preferred. McClelland and Stewart, Toronto, Ont. 198 p.

Phillips, G. L., D. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated fresh waters. Aquat. Bot. 4: 103–126.

Pringle, J. S. 1980. An introduction to wetland classification in the Great Lakes region. Royal Botanic Gardens Bull. No. 10, Hamilton, Ont.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Schaffner, W. R., and R. T. Oglesby. 1978. Limnology of eight Finger Lakes: Hemlock, Canadice, Honeoye, Kueka, Seneca, Owasco, Skaneateles and Otisco, p. 313–470. *In* J. A. Bloomfield [ed.] Lakes of New York State. Vol. 1. Ecology of the Finger Lakes. Academic Press, New York, NY.

Scoggan, H. J. 1978. The flora of Canada. 4 volumes. National Museum of Natural Sciences, Ottawa, Ont.

Sly, P. G. 1986. Review of postglacial environmental changes and cultural impacts in the Bay of Quinte, p. 7–26. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Smith, R. L. 1980. Ecology and field biology. Harper and Row, New York, NY.

Sokal, R. R., and P. H. Sneath. 1973. Numerical taxonomy. W. H. Freeman, San Francisco, CA.

Sparling, J. H. 1979. Wetland panorama. Ont. Nat. 19(2): 10–17.

Spence, D. H. M. 1975. Light and plant response in fresh water, 93–134. *In* G. E. Evans, R. Bainbridge, and O. Rackham [ed.] Light as an ecological factor. Blackwell Scientific Publications, Oxford.

Taylor, G. J., and A. A. Crowder. 1983. Uptake and accumulation of heavy metals by *Typha latifolia* in wetlands of the Sudbury, Ontario, region. Can. J. Bot. 61(1): 63–73.

Terasmae, J., and E. Mirynech. 1964. Post glacial chronology and the origin of deep lake basins in P. Edward Co. Ontario. Great Lakes Res. Div. Univ. Mich. Ann Arbor Publ. 11: 161–169.

Van der Valk, A. G., and C. B. Davis. 1978. Primary production of prairie glacial marshes. *In* R. E. Good, D. F. Whigham, and R. L. Simpson [ed.] Freshwater wetlands: ecological processes and management potential. Academic Press, New York, NY.

Weller, M. W. 1981. Freshwater marshes. Ecology and wild life management. University of Minnesota Press, Minneapolis, MN. 146 p.

Whigham, D. F., J. McCormick, R. E. Good and R. L. Simpson. 1978. Biomass and primary production in freshwater tidal wetlands of the middle Atlantic coast, p. 3–20. *In* R. E. Good, D. F. Whigham, and R. L. Simpson. Freshwater wetlands: ecological processes and management potential. Academic Press, New York, NY.

Wood, R. D. 1975. Hydrobotanical methods. University Park Press, Baltimore, MD.

Effect of Light Climate, Photosynthetic Capacity, and Respiration on Gross Integral Primary Production and Net Primary Production Potential in the Bay of Quinte, Lake Ontario

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Millard, E. S. 1986. Effect of light climate, photosynthetic capacity, and respiration on gross integral primary production and net prin.ary production potential in the Bay of Quinte, Lake Ontario, p. 128–138. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Primary production, chlorophyll *a* (Chl *a*), light extinction, mixing depths, and community respiration were measured throughout the Bay of Quinte, Lake Ontario, from 1973 to 1982. Model estimates of hourly integral primary production (ΣA) agreed closely with measured values using a shipboard incubator. Most of the variance (82.8%) was explained by $P_{max} \cdot$ Chl a/ε_{PAR}, the ratio of standing crop times its collective photosynthetic capacity over the extinction coefficient for photosynthetically available radiation. Chl *a* had an important effect on light penetration throughout the bay. Nonalgal sources of light extinction (ε_w) were high in the upper bay ($0.92 \cdot m^{-1}$) but declined in the lower bay ($0.43 \cdot m^{-1}$). High values for ε_w and ε_s, the self-shading coefficient (0.023 ln units · mg Chl $a^{-1} \cdot m^{-2}$), reduced the euphotic zone content of Chl *a* (ΣB) compared with other lakes. This negative effect on ΣA was offset by high values for P_{max} (3–7 mg C · mg Chl $a^{-1} \cdot h^{-1}$). Prior to phosphorus control, values for ΣB and Chl *a* reached theoretical maxima in the upper bay. The underwater light climate had become limiting to further increases in standing crop due to high light extinction caused by high phosphorus loading. In contrast, the seasonal trend in vertical mixing depths controlled the potential for net primary production in the lower bay.

La production primaire, la teneur en chlorophylle *a* (Chl *a*) l'extinction lumineuse, la profondeur de mélange et la respiration ont été déterminées dans toute la baie de Quinte (lac Ontario) de 1972 à 1982. Les estimations par modèle de la production primaire intégrée sur une base horaire (ΣA) correspondent de près aux valeurs déterminées à l'aide d'une étuve à bord. La plus grande partie de la variance (82,8 %) s'expliquait par $P_{max} \cdot$ Chl a/ε_{PAR}, le rapport entre la biomasse multipliée par la capacité photosynthétique collective et le coefficient d'extinction pour le rayonnement photosynthétiquement disponible. La teneur en Chl *a* avait un effet important sur la pénétration de la lumière dans les eaux de toute la baie. L'extinction lumineuse non provoquée par les algues (ε_w) était élevée dans la partie supérieure de la baie (0,92 m^{-1}), mais plus faible dans la partie inférieure ($0{,}43 \cdot m^{-1}$). Aux valeurs élevées de ε_w et de ε_s, le coefficient d'auto-ombrage (0,023 unité ln · mg Chl $a^{-1} \cdot m^{-2}$), la teneur en Chl *a* (ΣB) de la zone euphotique était faible comparativement à celles d'autres lacs. Cet effet négatif sur ΣA était compensé par des valeurs élevées de P_{max} (3–7 mg C · mg Chl $a^{-1} \cdot h^{-1}$). Les valeurs de ΣB et de Chl *a* avaient atteint leur maximum théorique dans la partie supérieure de la baie avant le début de la lutte contre le phosphore. Le régime photique sous-marin était devenu un facteur limitatif de toute augmentation ultérieure de la biomasse à cause de l'importante extinction lumineuse découlant de la charge élevée de phosphore. En revanche, dans la partie inférieure de la baie, l'allure saisonnière du mélange des eaux régissait la capacité de production primaire nette.

Introduction

The key to growth and survival of phytoplankton populations is the balance achieved between photosynthetic gain and respiratory loss of carbon over the mixed layer. The main purpose of this paper is to show how properties of the phytoplankton community such as size of standing crops (chlorophyll *a* (Chl *a*)), photosynthetic capacity and respiration rates, interacted with physical environmental factors such as irradiance, mixed depth, and light extinction to influence this balance seasonally in the Bay of Quinte. The critical-depth model of Talling (1971) was used to assess when the interaction of these factors over the season favoured net column photosynthesis.

In another paper in this issue, Millard and Johnson (1986) present seasonal trends for chlorophyll *a*, primary production rates, and light extinction (1972–82) in the Bay of Quinte. These authors used monthly and seasonal means to show how variables such as temperature, flow, and phosphorus loading controlled total seasonal primary productivity. However, they did not explain the spatial or temporal importance of properties of the phytoplankton community that contributed to short-term variability in primary production. In this paper the semiempirical model of Talling (1957b) describing integral photosynthesis was used to assess the relative importance of key determinants of this process.

Potential growth-limiting factors for phytoplankton differed markedly between the upper and lower regions in the Bay of Quinte. The upper bay is shallow and well-mixed with high phosphorus concentrations and a shallow euphotic depth. In contrast, the lower bay is deep with lower phosphorus concentrations and a deeper euphotic zone. In the lower bay, the underwater light climate is controlled by seasonal changes in mixing depth rather than changes in euphotic zone depth due to changes in algal density as in the upper bay.

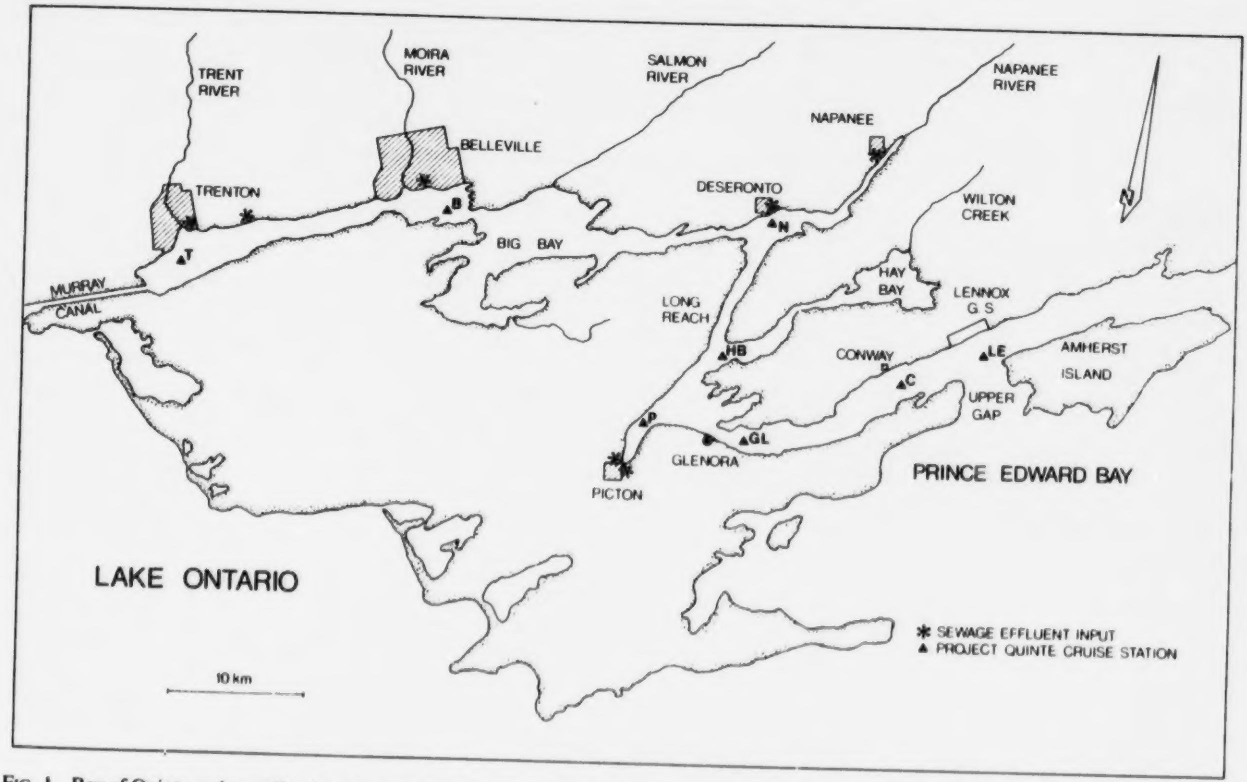

FIG. 1. Bay of Quinte and sampling locations; upper bay stations are T, B, and N, middle bay stations are HB and P, and lower bay stations are GL, C, and LE.

Materials and Methods

Sampling

Weekly sampling cruises were made from early May until the end of September or mid-October from 1972 to 1982. In some years, up to eight stations were visited throughout the bay, but five main stations (B, N, HB, GL, C) were sampled each season (Fig. 1). Greater detail on sampling and primary methods can be found in Millard and Johnson (1986).

Chlorophyll *a*

Composite water samples for Chl *a* analyses were collected through a depth equal to twice the Secchi disc visibility to approximate the depth of the euphotic zone. Aliquots (0.2–1.0 L) were filtered through GF/C glass-fibre filters (Whatman Co.), frozen, and analyzed later by the water Quality Branch, Environment Canada (for methods, see Environment Canada 1979). This method was used from 1977 to 1982. In earlier years (1973–76), samples were filtered through 1.2-μm membrane filters (Millipore Co.), frozen, and analyzed later at the Ontario Ministry of the Environment Laboratory, Rexdale, Ont. (Ministry of the Environment 1981) (see Millard and Johnson 1986 for comparison of methods). No chlorophyll data were available in 1972.

Light Extinction and Irradiance

Profiles of downwelling irradiance were measured with a submarine photometer equipped with a selenium photocell, cosine collector, and neutral-density, diffusing filter but no colour filters (model 268WA310, Kahl Scientific Inst. Co., San Diego, CA). The photocell had a relatively constant response over most of its range of spectral sensitivity (400–700 nm). Comparisons were made at various stations throughout the 1976, 1977, and 1978 field seasons with a quantaspectrometer (model QSM 2420, Incentive Research and Development, Sweden). The quantaspectrometer provided a trace of spectral distribution of quanta in the 400–700 nm range that was divided into three main spectral blocks. Areas in each block and for the whole visible range were integrated planimetrically and used to determine extinction coefficients for total (ε_T 400–700 nm), blue (400–500 nm), green (500–600 nm), and red light (600–700 nm). Vertical extinction coefficients were calculated according to Vollenweider (1974). Extinction coefficients for total visible light measured with the photometer (ε_{PAR}) compared well with those measured by the spectroradiometer (ε_T). There was no significant difference between estimates from different stations during 1977 and 1978 using a paired *t*-test ($n = 87$, $P = 0.01$). The mean ratio for $\varepsilon_{PAR}/\varepsilon_T$ was 1.01 ± 0.16 ($n = 121$). When the 1976 spectroradiometer data were included, there was a significant difference ($P = 0.05$) between the two estimates although the mean ratio was not that much higher (1.07 ± 0.11, $n = 35$). Data from 1976 contained more high values ($>2.0 \cdot m^{-1}$) than the other years, suggesting that ε_{PAR} values may have been slight overestimates when extinction was high. Overall, ε_{PAR} was probably an accurate estimate of extinction of total visible light.

Incident radiation was measured continuously with a pyranometer (Kipp and Zonen, Netherlands) located in the vicinity of the Ontario Ministry of Natural Resources, Fisheries Research Station, Picton, Ont. Subsurface irradiance of photosynthetically available radiation (PAR) was calculated assuming that PAR was 46% of total measured radiation and reflection losses were 10% (Vollenweider 1974).

Primary Production

Primary production was measured using the light- dark bottle oxygen method in a shipboard incubator exposed to sunlight. A light gradient was made by varying the number of sheets of neutral-coloured plastic over each of five chambers. The sixth chamber was left uncovered to represent surface conditions.

Two light and two dark bottles (300 mL BOD) were incubated horizontally in each chamber. The oxygen concentration at the start of incubations was measured. Community respiration (R_{com}) was calculated from the average of oxygen changes in all dark bottles. Bottles were incubated 3–4 in the upper bay and 4–5 in the lower bay. Nitrogen gas was bubbled through the water before bottles were filled to reduce oxygen concentration to 40–50% of saturation and thus minimize loss of oxygen in light bottles. Stations were always visited in the same order to keep the time of day constant for each station. Most of the incubations were conducted between 08:00 and 16:00 (Eastern Standard Time), and incubations for some of the stations (B, GL, C, LE) were always between 09:00 and 15:00.

A depth profile of in situ gross primary production rates was simulated by plotting volume-based rates from each chamber at a depth determined from the extinction coefficient and percent light transmission for that chamber. These profiles were integrated to get mg C · m $^{-2}$ · h $^{-1}$ using a photosynthetic quotient of 1.25 (Ryther 1956).

Primary Production and Critical Depth Models

Hourly integral photosynthetic rates (A) were also calculated using a modification of Talling's (1957b) semiempirical model

$$\Sigma\Sigma A = \frac{\text{Chl } a \cdot P_{max}}{\varepsilon_{PAR}} \cdot \ln\left[\frac{I'_0}{0.5 I_K}\right].$$

Talling used the extinction coefficient for the most penetrating spectral block (ε_{min}) times a constant factor a to describe the attenuation of PAR. In this study, estimates of light extinction made with the photometer agreed closely with a more precise measure of extinction of PAR. As a result, ε_{PAR} measured with the photometer was used routinely in the model calculations.

The critical depth model of Talling (1971) was used to assess when conditions of irradiance, mixing depth, light extinction, respiration, and photosynthetic capacity were favourable for net column photosynthesis over a 24-h period. The critical depth model was derived from Talling's (1957b) model used to calculate daily rates of gross photosynthesis for the water column

$$\Sigma\Sigma A = \frac{\text{Chl } a \cdot P_{max} \cdot \ln 2}{\varepsilon_{PAR}} \cdot [\text{L.D.H.}]$$

and

$$[\text{L.D.H.}] = 0.9 \cdot \Delta t \left[\frac{\ln \bar{I}_0 - \ln 0.5 I_K}{\ln 2}\right].$$

At the column compensation point, gross photosynthesis and respiration for the mixed depth are equal so that $\Sigma\Sigma A$ is equal to Chl $a \cdot r \cdot P_{max} \cdot Z_m \cdot 24$ h. The equations can be rearranged to solve for a critical value (q_c) that compares irradiance and the underwater light climate against relative respiration rates to determine when net photosynthesis is possible so that at the column compensation point:

$$q_c = \frac{[\text{L.D.H.}]}{\varepsilon_{PAR} Z_m / \ln^2} = 24\, r.$$

Data for day length (Δt) were obtained from meteorological tables (Smithsonian Institution 1951). The value 0.9 is an empirical factor used to correct for the effectiveness of daylength on dull days and the slight overestimates that arise from using the mean incident light intensity during the day ($\bar{I}'_o$) (Talling 1957b). Since ε_{PAR} was used instead of $\varepsilon_{min} \cdot a$, the solution for q_c is compared with 24 r', *not* $a \cdot 24r'$ as originally indicated by Talling. The proportionality between the critical ratio and respiration is not changed because ε_{PAR} is greater than ε_{min} and the effect of deleting a cancels out.

Millard and Johnson (1986) used constant values of I_K of 2.5 and 3.0 g cal · cm $^{-2}$ · h $^{-1}$ for the lower and upper bays, respectively, in their calculation of $\Sigma\Sigma A$ using Talling's model. Graphically, I_K can be determined from photosynthetic rate versus irradiance plots as the irradiance where extrapolation of the linear portion of the curve intersects the asymptote or light-saturated rate. However, it was difficult to obtain accurate weekly estimates of I_K from the incubator data because in most years there was insufficient data for the light-limited portion of the production profile. Values for I_K derived graphically were quite variable but indicated that a mean I_K for May to September was in the range 2.0–4.0 g cal · cm $^{-2}$ · h $^{-1}$.

In 1981 and 1982, irradiances in two of the incubator chambers were more consistently in the linear portion of the photosynthesis–light curve than in other years. The slope of the line between primary production rates in these two chambers was extrapolated to light saturation and used to calculate I_k based on the irradiance during incubation.

Mixed Depth and Column Stability

Depth profiles of temperature throughout the water column were obtained with a Hydrolab (model TD02 Austin, TX) temperature–oxygen probe. Density was calculated every 0.5 m and the mixing depth taken as the depth of the maximum density gradient. A criterion of 0.08 kg · m $^{-3}$ · m $^{-1}$ was chosen as the minimum density gradient required to delineate a mixed depth. At 10°C, this criterion was met with a thermal gradient of 0.8–0.9°C · m $^{-1}$, while at 20°C, 0.4°C · m $^{-1}$ was sufficient. Our criterion for choice of a mixed depth was similar to other studies (Harris et al. 1980; Reynolds and Wiseman 1982; Reynolds et al. 1984) If the density gradient was <0.08 kg · m $^{-3}$ · m $^{-1}$ the mixing depth was considered to be equal to station depth. Thermal stability in the water column and thus resistance to mixing was characterized by N^2, the solution of the Brunt–Väsälä equation for frequency of vertical oscillation of a water column for a given displacement from equilibrium (Phillips 1966; Harris 1983):

$$N^2 = (g/\rho)\ (\delta\rho/\delta Z)\ s^{-2}$$

where g is gravitational acceleration, ($\delta\rho/\delta Z$) is the mean density gradient through a water column of depth Z, and ρ is the mean density of that water column. Water column depths used to calculate N^2 were 9, 9, 18, 27 and 54 m for stations HP, P, GL, C, and LE, respectively.

Symbols and Abbreviations

Chl a	Chlorophyll a (mg · m $^{-3}$)
ΣB	Euphotic zone content of Chl a (mg · m $^{-2}$)
ΣB_{max}	Theoretical upper limit to ΣB; calculated in this study as $3.9/\varepsilon_s$
ε_{PAR}	Vertical extinction coefficient for visible light (400–700 nm) measured with a photometer (m $^{-1}$)

ε_T	Vertical extinction coefficient for visible light measured with a quantaspectrometer
ε_{min}	Vertical extinction coefficient for the most penetrating spectral block
ε_w	Background light extinction coefficient (m^{-1}); the *y*-intercept in the ε_{PAR} vs. Chl *a* regression
ε_s	Self-shading coefficient, increment in ε_{PAR} for a unit increase in Chl *a* (ln units $\cdot$ mg Chl $a^{-1} \cdot m^{-2}$)
A_{max}	Light-saturated rate of primary production (mg $C \cdot m^{-3} \cdot h^{-1}$)
ΣA	Hourly integral rate of primary production (mg $C \cdot {}^{-2} \cdot h^{-1}$)
P_{max}	Photosynthetic capacity of the phytoplankton community from A_{max}/Chl *a* (mg C $\cdot$ mg Chl $a^{-1} \cdot h^{-1}$)
[L.D.H.]	Light–division–hours (see Materials and Methods)
I'_o	Irradiance of photosynthetically available radiation (PAR) just below the water surface during primary production incubations (g cal $\cdot cm^{-2} \cdot h^{-1}$)
$\bar{I}_o$	Mean subsurface irradiance over the day length Δt (g cal $\cdot cm^{-2} \cdot h^{-1}$)
I_K	Irradiance where light saturation of photosynthesis begins (g cal $\cdot cm^{-2} \cdot h^{-1}$)
Z_{eu}	Depth of euphotic zone, 1% penetration of subsurface irradiance (m)
Z_m	Depth of vertical mixing (m)
Z_{od}	Optical depth of mixed layer ($\varepsilon_{PAR} \cdot Z_m / \ln 2$)
R_{com}	Community respiration rates (mg $O_2 \cdot m^{-3} \cdot h^{-1}$)
R_{Chl}	R_{com} expressed per unit Chl *a* (mg $O_2 \cdot$ mg Chl $a^{-1} \cdot h^{-1}$)
r'	Relative respiration rate from R_{com}/A_{max}
r	Correlation coefficient

Results

Model Estimates of ΣA

Overall, excellent agreement was found between ΣA measured in the incubator and ΣA calculated with Talling's model using constant values for I_K (ΣA model $= 1.42 + 0.97\ \Sigma A$ incubator, $r = 0.93$, all weekly values $n = 1578$) (Fig. 2).

Monthly means for I_K estimated from the 1981–82 data ($n = 137$) were 2.12 ± 1.22, 2.74 ± 1.42, 3.22 ± 1.35, 3.59 ± 1.26, and 2.71 ± 1.33 g cal $\cdot cm^{-2} \cdot h^{-1}$ for May to September, respectively. The seasonal average of 2.88 g cal $\cdot cm^{-2} \cdot h^{-1}$ based on these estimates was very close to the constant values for I_K used in model calculations.

The constant I_K values compare favourably with average values (2.0–3.0 g cal $\cdot cm^{-2} \cdot h^{-1}$) found in studies done at similar temperatures (Bindloss 1974; Jewson 1976; Jones 1977; Harris 1978). In addition, the chosen I_K values gave the best fit in regressions with measured ΣA at each station. Although this criterion was somewhat subjective, since others had found close agreement between measured and calculated ΣA with Talling's model (Jewson 1976; Jones 1977), it was further evidence that our I_K values were reasonable estimates. The direct estimates of I_K were too variable and not based on sufficient data to show a difference in I_K between stations. However, the consistently lower temperatures in the lower bay and the dependence of I_K on temperature (Talling 1957a) suggested that lowering I_K slightly for the lower bay was justified.

Using the monthly estimates of I_K would have introduced a seasonal effect of temperature on I_K and thus ΣA but would have had only a slight effect overall. For example, at station B ($n = 234$, 1972–82), using the monthly I_K values would have increased model estimates of ΣA by an average of only 3.0% and lowered model estimates of ΣA by 4.8% at station C compared with results with the constant value.

Importance of Determinants of ΣA

The ratio Chl $a \cdot P_{max}/\varepsilon_{PAR}$ was the most important component of Talling's model in estimates of ΣA. In a simple linear regression this ratio explained 82.8% of the variance in incubator estimates of ΣA using all weekly data for all stations ($\Sigma A = 5.15 + 2.45$ Chl $a \cdot P_{max}/\varepsilon_{PAR}$, $r = 0.91$, $n = 1616$, $P = 0.01$). This indicates that overall the light function part of the model was not that important in model estimates of ΣA. Integral production was insensitive to fluctuations in irradiance during midday incubations because intensities were usually well above I_K. The I_K values used in the model appear to be reasonable estimates, and over a season probably introduced little error into model estimates of ΣA. However, on a weekly basis, choice of a constant I_K may have caused some serious discrepancies between observed and modelled ΣA. The monthly I_K estimates correspond to the seasonal trend in water temperatures and indicate that I_K was lower in the spring and higher in the summer than the constant values. Consequently, model estimates may have underestimated ΣA in the spring and overestimated in the summer.

The light-saturated rate of primary production A_{max} is equal to the product of standing crop as measured by Chl *a* and its collective photosynthetic capacity (P_{max}, mg C $\cdot$ mg Chl $a^{-1} \cdot h^{-1}$). A_{max} was positively related to Chl *a* (Millard and Johnson 1986) indicating that changes in standing crop, not P_{max}, probably accounted for more of the variability in ΣA. The relationship between A_{max} and Chl *a* uncorrected for phaeopigments was $A_{max} = 4.86 + 3.96$ Chl a ($r = 0.92$, $n = 786$, $P < 0.01$). Using corrected Chl *a* would have made only a slight difference to the slope in this relationship (4.10) and increased monthly means for P_{max} by about 15–20%.

P_{max} fluctuated between 3 and 7 mg C $\cdot$ mg Chl $a^{-1} \cdot h^{-1}$ from June to September throughout the bay and at times was remarkably constant throughout this period (Fig. 3). P_{max} was usually lower at peak Chl *a* and declined during September in some years (1977, 1978). P_{max} was variable between both stations and years with no clear difference between upper and lower bay. However, A_{max} was influenced more by changes in Chl *a* in the upper bay than in the lower bay because of the dramatic summer increases in algal standing crop that occurred without large changes in P_{max}. For example, comparing seasonal variances in Chl *a* (1977–82) between stations B and C with a simple *F*-test showed highly significant differences ($P = 0.01$) in each year (*F* range 7.6–73.2). The differences were still highly significant if only the period of higher Chl *a* levels (July–September) was considered. In contrast, P_{max} was more variable in the lower bay and, therefore, of more relative importance in determining variation in A_{max} and thus ΣA. The *F*-tests on the seasonal variances in P_{max} at stations B and N compared with C showed significantly higher variance in the lower bay in three of the six years ($P = 0.05$).

Variability in P_{max} was not consistently well explained by other variables in linear regressions. The relationship between log P_{max} and log temperature was significant in some earlier years but was barely significant or insignificant in others. A significant relationship between these variables was found for the 1973–77 period (log $P_{max} = -0.028 + 0.657$ log temp., $r = 0.43$, $n = 861$, $P = 0.01$) but not for the 1978–82 period.

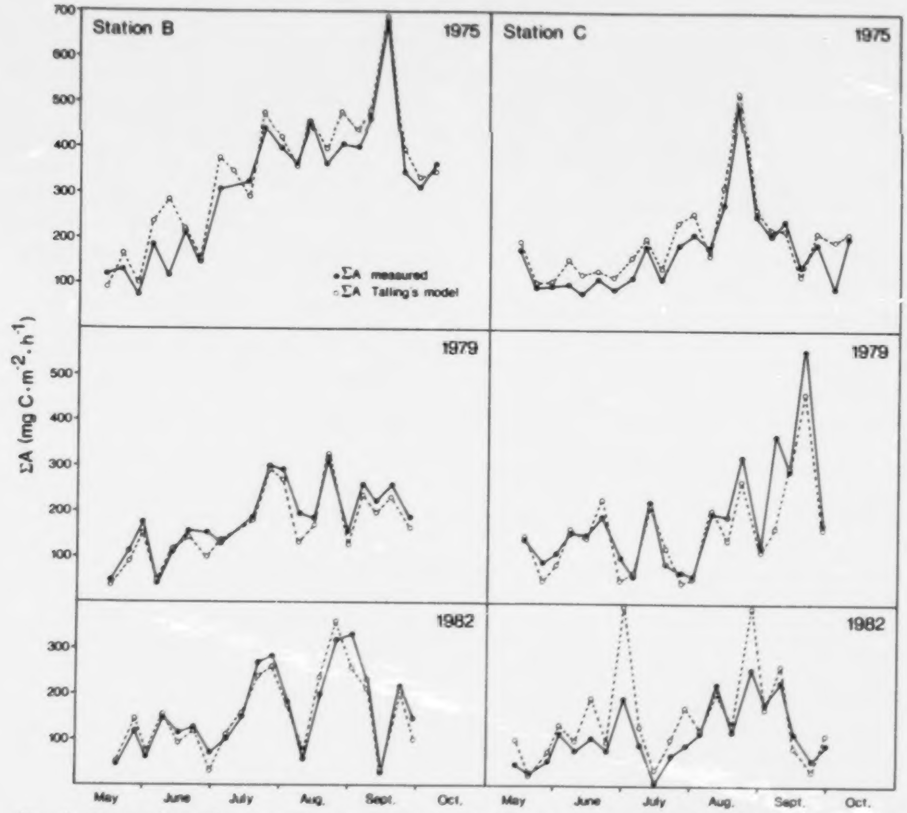

FIG. 2. Comparison of measured and predicted hourly integral primary production (ΣA) at an upper (B) and lower (C) bay station.

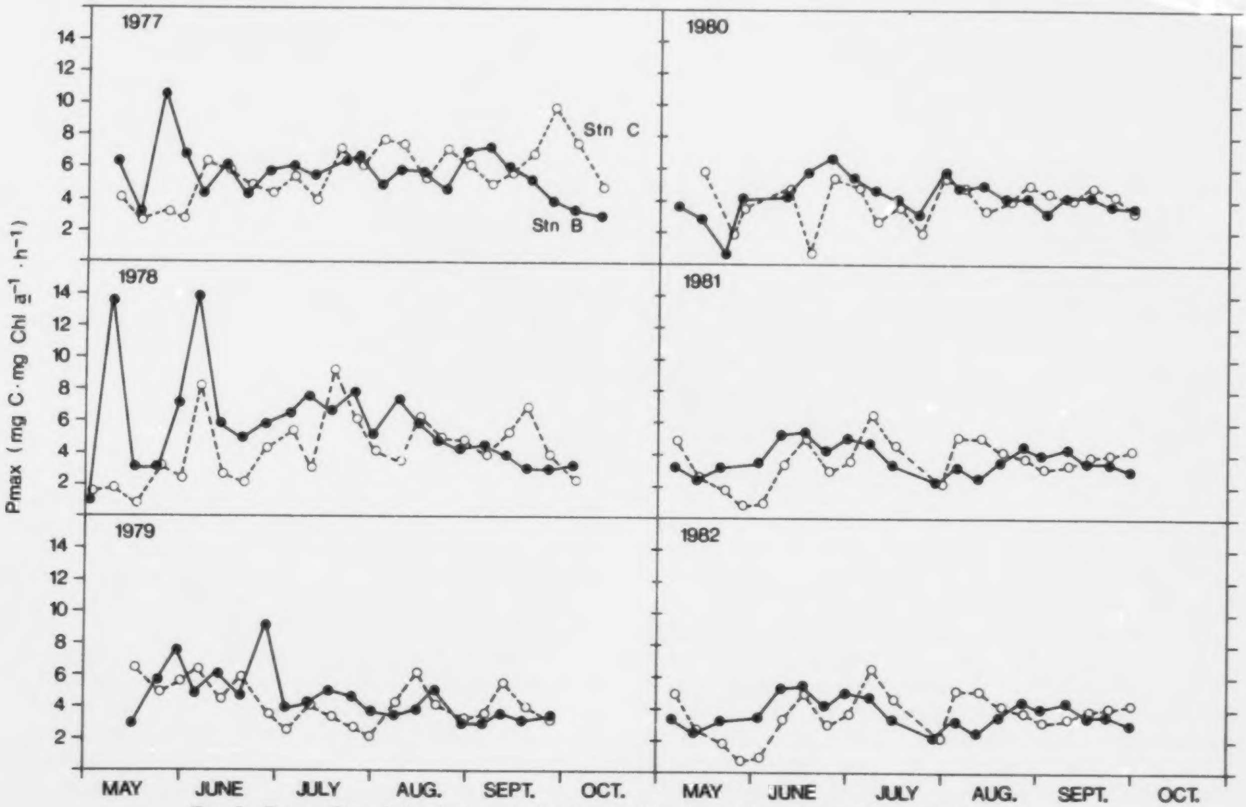

FIG. 3. Seasonal trends in photosynthetic capacity (P_{max}) at stations B and C from 1977 to 1982.

TABLE 1. Results of regressions of ε_{PAR}, ε_T, and ε_{min} vs. Chl *a* (uncorrected for phaeopigments) where $\varepsilon_{PAR} = \varepsilon_w + \varepsilon_s \cdot$ Chl *a* (*significant $P = 0.05$; all other regressions significant $P = 0.01$).

Stations	ε_w	ε_s	*r*	*n*
Photometer ε_{PAR}				
T	0.92	0.031	0.89	63
B, N	0.92	0.024	0.86	250
HB, P	0.68	0.023	0.89	172
GL, C, LE	0.43	0.023	0.75	303
Quantaspectrometer ε_{min}				
T, B, N	0.75	0.020	0.85	29
HB, P	0.72	0.014	0.47*	19
T, B, N, HB, P	0.71	0.019	0.77	48
GL, C, LE	0.34	0.022	0.63	48
Quantaspectrometer ε_T				
T, B, N	0.89	0.020	0.89	29
HB, P	0.80	0.018	0.57	19
T, B, N, HB, P	0.83	0.020	0.82	48
GL, C, LE	0.44	0.024	0.67	48

TABLE 2. Average euphotic zone depths (m) in the Bay of Quinte (all weekly values averaged for specified periods).

Station	Mean	SD	Range
Pre-phosphorus control, 1972–77			
T	2.65	0.87	1.40–4.30
B	2.71	0.95	1.45–5.50
N	2.73	0.94	1.22–5.80
Post-phosphorus control, 1978–82			
T	3.37	0.88	1.70–3.80
B	3.45	1.00	1.55–5.10
N	3.21	1.04	1.40–5.50
All years, 1972–82			
HB	3.63	1.16	1.70–11.3
P	4.27	1.15	1.62–7.43
GL	5.66	1.36	3.24–10.47
C	7.73	1.69	4.19–13.54
LE	9.01	2.22	5.01–16.45

Influence of Algal Standing Crops on Light Extinction

The regressions of vertical extinction coefficients for photosynthetically available radiation (ε_{PAR}) on Chl *a* were highly significant throughout the bay (Table 1). The intercepts (ε_w,' background light extinction) and slopes (ε_s,' self-shading coefficient) in these regressions are fundamental to defining ΣB_{max}, the theoretical upper limit to euphotic zone content of Chl *a* (Talling, 1960, 1965). Originally, ε_s was defined by Talling in terms of ε_{min}, the extinction coefficient for the most penetrating part of the spectrum. Estimates of ε_s using ε_{min} from spectroradiometer measurements indicated that there was little difference from estimates with ε_{PAR}.

On most occasions, green light was the most penetrating spectral block (ε_{min}) but the differences from extinction coefficients for red light were slight in the more productive upper and middle bay. In 19 of 167 profiles done for spectral analysis, red light was ε_{min} and only two of these were in the lower bay. A shift from green to red light as ε_{min} in productive lakes has also been found by others (Ganf 1974; Bindloss 1976; Jewson 1977). The poorer relationship and lower ε_s using spectroradiometer data at the middle bay stations were likely due to the smaller number of measurements. When data from these stations were combined with upper bay data, no difference in either ε_s or ε_w was noted compared with upper bay data only. An average for ε_s throughout the bay was between 0.020 and 0.024 but an average value may have been higher at the extreme upper end of the bay (station T).

The *y*-intercept (ε_w) in the ε_{PAR} versus Chl *a* regressions was an average estimate of background light extinction or extinction due to sources other than Chl *a*. A well-defined gradient in ε_w from the upper ($0.92 \cdot m^{-1}$) though the middle ($0.68 \cdot m^{-1}$) to the lower bay ($0.43 \cdot m^{-1}$) was evident.

Euphotic Zone Depth and its Chl *a* Content

Euphotic zone depths (Z_{eu}) were shallowest in the upper bay, especially before phosphorus control, but were deeper after controls were started (Table 2). There was a distinct gradient to deeper Z_{eu} progressing from upper to lower bay. Talling (1965) defined Z_{eu} as b/ε_{min} ($b = 3.7$), and this relationship has been found to be applicable for a variety of lakes (Talling 1965; Ganf 1974; Bindloss 1976; Robarts 1979). The appropriate value for *b* is important because it is used to derive ΣB_{max}, the maximum amount of Chl *a* that can exist in Z_{eu} and thus contribute to production in the water column. Comparison of Z_{eu} estimated from ε_T and b/ε_{min}, measured with the spectroradiometer, indicated that a value of 3.9 for *b* was more appropriate for the Bay of Quinte, similar to other studies (Jones 1977; Jewson 1977). According to Talling (1965), ΣB_{max} occurs when ε_{PAR} is due only to Chl *a* and is equal to b/ε_s or $3.9/0.023 = 170$ mg Chl $a \cdot m^{-2}$ for the Bay of Quinte. At ΣB_{max}, complete self-shading occurs and further increases in Chl *a* have no effect on ΣB because of the opposing effect of reduced Z_{eu}.

The values for ε_w for the upper, middle, and lower bay represented an additional 40, 30, and 19 $mg \cdot m^{-2}$ of euphotic zone Chl *a* ($\varepsilon_w/\varepsilon_s$). Estimates of ΣB_{max} that subtract the chlorophyll equivalent of ε_w would be 130, 140, and 151 $mg \cdot m^{-2}$ for the upper, middle, and lower bay, respectively. Measured levels of ΣB met or exceeded these levels most frequently in the upper bay during the pre-phosphorus control period.

Water Column Stability, Mixing, and Optical Depths

Stratification was most stable at station HB in the middle bay, as indicated by the higher mean values for N^2 from June through August ($921-1754 \times 10^{-6} \cdot s^{-2}$) when stratification occurred (Table 3). Mixing depths (Z_m) increased and stability during stratification decreased, progressing lakeward from station HB. Usually, Z_m deepened and N^2 declined as stratification weakened in late August and September (Fig. 4). However, the deeper, more consistent Z_m in the summer at stations GL (10–15 m) and C (15–20 m) were often associated with seasonal maxima for N^2. The length of time that full circulation (Z_m = station depth) persisted in the spring was longer for the deeper stations. At HB, Z_m shortened through May to minimum values in June with similar conditions occurring at GL. At stations C and LE it was early July before Z_m declined and N^2 values were much lower than at the shallower stations.

Optical depth (Z_{od}) is a dimensionless quantity ($\varepsilon_{PAR} \cdot Z_m/\ln 2$) that describes the effects of both light extinction and mixing depth on the underwater light climate (Talling 1971). The importance of ε_{PAR} and Z_m to Z_{od} differed from upper and lower bay (Table 4). In the upper bay, ε_{PAR} increased with algal standing crops to produce an optically deep water column in spite of the shallow depth. For example, prior to phosphorus control, summer Z_{od} in the upper bay was as high at times as the middle and lower bay when Z_m was much deeper. Summer values for Z_{od} in

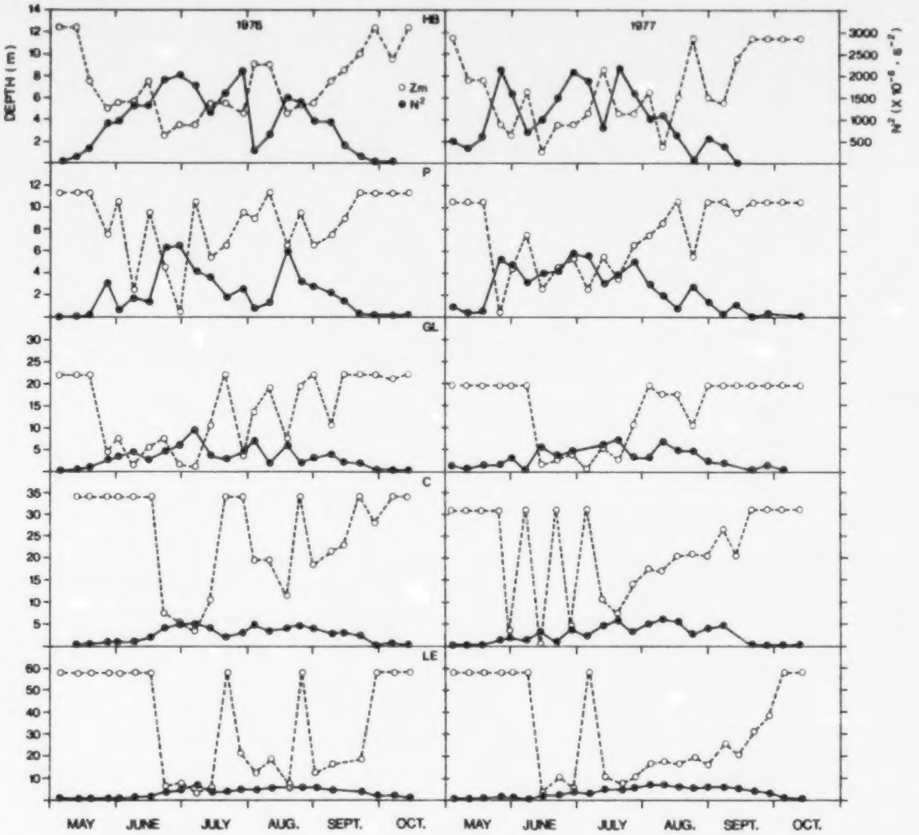

FIG. 4. Seasonal trends in mixing depths (Z_m) and water column stability (N^2) in the middle and lower Bay of Quinte in 1976 and 1977.

TABLE 3. June to August averages for mixing depth (Z_m) and N^2 at the middle and lower bay stations.

	HB		P		GL		C		LE	
Year	Z_m	N^2	Z_m	N^2	Z_m	N^2	Z_m	N^2	Z_m	N^2
1972	6.4	1443	6.2	925	9.5	553	14.8	411		
1973	6.2	1396	4.9	1012	10.7	493	14.7	514		
1974	6.7	921	7.4	417	11.2	464	17.3	355		
1975	6.7	1177	6.4	811	10.5	548	16.1	512	16.7	299
1976	5.5	1351	7.3	776	10.1	436	20.7	343	28.5	218
1977	5.2	1150	6.2	855	10.1	415	17.4	367	22.0	229
1978	6.6	1185	4.6	646	12.4	466	18.2	394	21.2	238
1979	5.8	1160			7.5	526	14.8	391		
1980	5.2	1064			11.7	551	17.3	421		
1981	5.0	1099			10.5	524	13.3	414		
1982	3.3	1754			8.9	647	13.4	296		
$\bar{x}$	5.7	1245	6.1	777	10.3	511	16.2	402	22.1	246

the upper bay declined after phosphorus control due to improved transparency (Millard and Johnson 1986). The advantage of deeper euphotic zone depth to Z_{od} in the lower bay was offset throughout much of the season by deep mixing, particularly in spring and fall when full column circulation existed. In addition, light attenuation was highest in the spring at station C. The onset of stratification by July in the lower bay was extremely important because it reduced Z_m and thus Z_{od}. Optical depth was at its maximum throughout the bay in September because ϵ_{PAR} remained high in the upper and middle bay and Z_m increased at all the deeper stations.

Respiration

Weekly estimates of community respiration rates (R_{com}) were quite variable. Errors in the detection of small changes in oxygen concentrations during short incubations were likely an important source of variability. However, when Chl *a* was higher during summer, changes in oxygen concentration were easily detected. Monthly means for R_{com}, specific respiration rates (R_{Chl}, mg $O_2 \cdot$ mg Chl $a^{-1} \cdot h^{-1}$), and respiration rates relative to A_{max} (r') were averaged over all years to determine seasonal and regional differences (Table 5). Values of R_{Chl} and r' were higher in the spring and in the lower bay, situations where Chl *a* was lowest. This suggested that there was a strong nonalgal component to R_{com} throughout the bay.

In an attempt to separate nonalgal contributions from R_{com}, monthly means for R_{com} were plotted against corrected Chl *a* for all stations averaged over the 1977–82 period (Fig. 5). The intercept in this regression (28.65 mg $O_2 \cdot m^{-3} \cdot h^{-1}$) is an estimate of R_{com} due to nonalgal sources, and the slope (1.48 mg $O_2 \cdot$ mg Chl $a^{-1} \cdot h^{-1}$) is the average R_{Chl}. High R_{com} in May compared with levels of Chl *a* show that background sources of respiration were higher at this time of the year than the seasonal estimate. Compared with measured monthly means of R_{com}, the *y*-intercept was high and would have accounted for at least 55% of R_{com} during the spring in the upper bay and 35% during the summer. In the lower bay this background rate could have made

TABLE 4. Monthly means for light extinction coefficients, mixing depths, and optical depths.

Period	Station	May			June			July			August			September		
		ε_{PAR}	Z_m	Z_{od}	ε_{PAR}	Z_m	Z_{od}	ε_{PAR}	Z_m	Z_{od}	ε_{PAR}	Z_m	Z_{od}	ε_{PAR}	Z_m	Z_{od}
1972–77	T	1.29	4.1	7.7	1.58	4.1	9.4	2.12	4.1	12.6	2.27	4.1	13.5	2.30	4.1	13.8
	B	1.21	5.4	9.5	1.48	5.4	11.6	2.03	5.4	15.8	2.29	5.4	17.9	2.28	5.4	17.9
	N	1.22	5.7	9.9	1.47	5.7	11.9	2.02	5.7	16.2	2.18	5.7	17.6	2.35	5.7	19.2
1978–82	T	1.19	3.7	6.2	1.11	3.7	5.9	1.46	3.7	7.7	1.75	3.7	9.4	2.06	3.7	10.7
	B	1.08	5.1	7.9	1.08	5.1	7.9	1.43	5.1	10.4	1.79	5.1	13.1	1.79	5.1	13.1
	N	1.04	5.4	8.1	1.21	5.4	9.4	1.75	5.4	13.6	1.90	5.4	14.7	1.92	5.4	15.0
1972–82	HB	1.06	7.2	11.8	1.06	4.5	7.1	1.39	5.1	9.9	1.51	7.2	15.7	1.70	9.2	19.4
	P	1.05	7.6	12.1	0.96	5.1	7.8	1.08	5.6	10.2	1.15	7.6	12.5	1.33	9.3	18.2
	GL	0.84	13.2	16.2	0.75	9.1	9.7	0.79	7.7	8.5	0.95	13.9	18.8	0.93	18.4	24.4
	C	0.70	23.7	22.7	0.59	20.8	17.2	0.62	11.9	10.1	0.62	16.6	14.7	0.61	23.0	20.1
	LE	0.67	39.2	35.9	0.53	31.0	23.6	0.55	16.6	12.3	0.51	18.8	13.7	0.49	27.8	18.6

TABLE 5. Monthly community (R_{com}), chlorophyll-based (R_{Chl}), and relative respiration rates (r') for the upper and lower bay.

Variable[a]	B					C				
	May	June	July	Aug	Sept	May	June	July	Aug	Sept
R_{com}	52	51	82	79	71	48	38	40	45	38
R_{Chl}										
Corrected	8.63	5.98	4.81	3.12	2.28	9.26	8.79	8.37	5.41	5.41
Uncorrected	6.73	4.86	3.76	2.54	1.98	5.59	5.59	5.51	3.97	4.19
r'	0.45	0.24	0.18	0.13	0.13	0.63	0.22	0.40	0.26	0.25

[a] R_{Chl} was averaged over the 1977–82 period. Values are calculated with Chl *a* corrected and uncorrected for phaeopigments. R_{com} and r' were averaged from 1972–82.

up 75% of R_{com}.

This background respiration made it difficult to equate estimates of r' to algal respiration during part of the season. A seasonal average for r' of 0.11 due to algae was determined from the ratio of the slopes from the R_{com} and A_{max} versus Chl *a* (corrected) regressions where $r' = 1.48\ \mathrm{mg\ O_2 \cdot mg\ Chl}\ a^{-1} \cdot \mathrm{h}^{-1} / 13.65\ \mathrm{mg\ O_2 \cdot mg\ Chl}\ a^{-}\text{-}1 \cdot \mathrm{h}^{-1}$. This estimate is in the upper range of values usually found for r' (Talling 1971). This may have resulted from collecting most of the data over a relatively warm and narrow temperature range. Weekly values of r' were often between 0.05 and 0.10 during the summer in the upper bay when background sources were relatively less important. For example, 43% of all the weekly estimates of r' in the upper bay were <0.10, and most of these occurred from July to September. A significant relationship between respiration rates and temperature was not found.

Interaction of Light Climate, Optical Depth, and Respiration and the Potential for Net Photosynthesis

When the critical ratio (q_c) calculated from the critical depth equation was less than $24r'$, the combination of environmental factors and physiological properties of the phytoplankton community was not favourable for net photosynthesis. Likewise, if q_c exceeded the critical value (2.4 if $r' = 0.10$), net photosynthesis was possible. The interaction of the variables determining q_c are illustrated in a plot of Z_{od} versus [L.D.H.] (Fig. 6). Values for the critical ratios determined by r' are indicated by the broken lines. Points falling above the critical line represent situations when net photosynthesis was not possible, and the opposite is true for points below the line. At $r' = 0.10$, net photosynthesis would have been unlikely anywhere in the bay during September under average light and mixing conditions. In the middle and lower bay prior to phosphorus control, an r' of less than 0.075 was required for net photosynthesis. Under average conditions, net photosynthesis was possible at all stations during the season at $r' = 0.05$.

Grand monthly means for ε_{PAR} and Z_m were obtained from Table 4. Monthly estimates of [L.D.H.] were based on daily radiation data from the 1977–82 period. The grand means for monthly [L.D.H.] from May to September were 42.3 ± 2.2, 43.5 ± 1.6, 44.9 ± 0.9, 38.7 ± 0.6, and 31.3 ± 2.8 in the upper bay. The means for [L.D.H.] were slightly higher in the lower bay because of the lower I_K and were 45.6, 47.2, 48.4, 42.0, and 34.4 from May to September. In the upper bay, pre- and post-phosphorus control periods were separated because ε_{PAR} declined significantly in the postcontrol period (Millard and Johnson 1986).

Discussion

Growth of phytoplankton communities is dependent on gross production summed for the euphotic zone balanced against community respiration. In the Bay of Quinte, P_{max} was a key determinant of integral production. Therefore, P_{max} was an important collective physiological property influencing the potential for growth of the phytoplankton community. Average values in the Bay of Quinte for P_{max} of 4–5 mg $\mathrm{C \cdot mg\ Chl}\ a^{-1} \cdot \mathrm{h}^{-1}$ appear to be in the upper range of values found in other temperate waters (Glooschenko et al. 1974; Jewson 1976; Harris 1978). A strong relationship between P_{max} and temperature was not evident in this study, but low P_{max} values often occurred during September when temperatures dropped. The relationship may have been poor because of the narrow temperature range for data collection compared with other studies (Bindloss 1974; Jones 1977). Average values for P_{max} in the Bay of Quinte agreed closely with the range of 12–15 mg $\mathrm{O_2 \cdot mg\ Chl}\ a^{-1} \cdot \mathrm{h}^{-1}$ at 20°C predicted by the relationship of Harris and Piccini (1977).

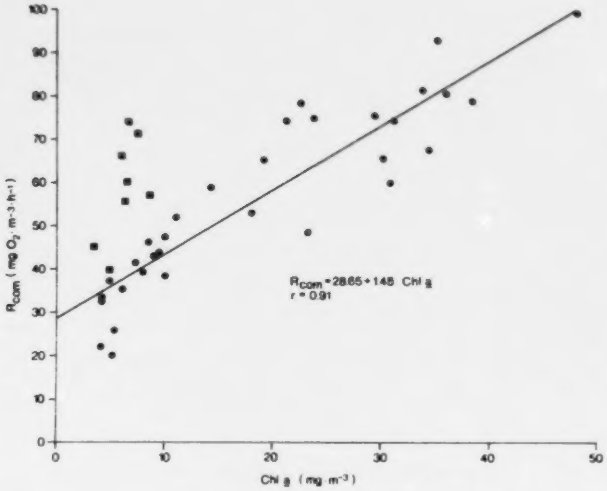

FIG. 5. Monthly means averaged from 1977 to 1982 for community respiration rates (R_{com}) vs. Chl *a* corrected for phaeopigments. The six highest May values (■) were not included in the regression.

The P_{max} was consistently high throughout the bay in spite of the differences in phosphorus concentrations (Robinson 1986) suggesting that nutrients were not limiting. Effects of nutrient limitations on P_{max} have been reported (Curl and Small 1965; Glooschenko and Curl 1971), but most studies suggest that temperature has a greater influence (Harris 1978; Falkowski 1981).

High ε_w and ε_s reduced ΣB compared with other waters. However, high values for P_{max} offset the potential negative effect that reduced euphotic zone content of chlorophyll would have had on integral photosynthesis. High P_{max} was probably due to both high nutrient supply and temperatures, particularly in the upper bay. As a result, values for A_{max} (Chl $a \cdot P_{max}$) and ΣA were among the highest found in the literature for productive, temperate-climate lakes (Millard and Johnson 1986). Differences in ΣA throughout the bay were slight considering the differences in volume-based measures of standing crop and production. In the lower bay, deeper Z_{eu} occurred in response to lower Chl *a* and ε_w. The increase in Z_{eu} compensated ΣA for lower A_{max} because of lower Chl *a* and a possible decline in P_{max} at the lower temperatures.

Seasonal constraints on production occurred by September because of the natural decline in effective irradiance ([L.D.H.]). Both day length (Δt) and the mean light intensity during the day ($\bar{I}_o$) determine [L.D.H.] and both declined significantly by September. Therefore, upper limits to $\Sigma\Sigma A$ changed seasonally because of geographic limitations on Δt and $\bar{I}_o$. However, adaptation to changing irradiance by lowering I_K would have partially offset the effect on [L.D.H.]. In the late spring and early summer when [L.D.H.] was highest, the upper limit to $\Sigma\Sigma A$ was probably set by the photosynthetic capacity (P_{max}) and euphotic zone content of Chl *a* (ΣB).

Parameters such as the self-shading (ε_s) and background light extinction (ε_w) coefficients were important properties of the phytoplankton community. They defined the euphotic zone content of Chl *a* (ΣB) and thus the amount of phytoplankton that could contribute to gross photosynthesis for the water column. Estimates of both ε_s and particularly ε_w in the upper bay were high compared with other bodies of water (Field and Effler 1983), thus reducing ΣB_{max}. Furthermore, ΣB_{max} and thus integral production were likely to vary depending on changes in species composition and their effect on ε_s (Kirk 1975a, 1975b).

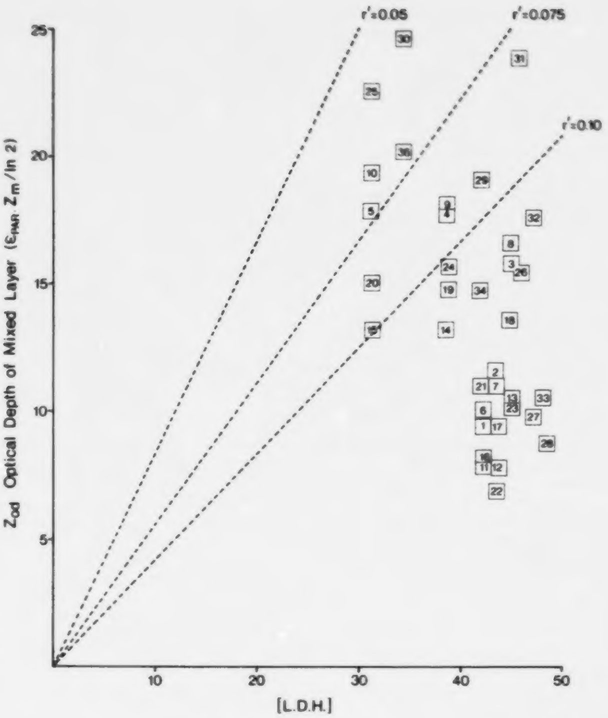

FIG. 6. Interaction of the logarithmic function of daily radiation [L.D.H.] and the optical depth of the mixed layer ($\varepsilon_{PAR} \cdot Z_m$/ln 2). Critical values of the ratio between these variables are shown by lines for different levels of the relative respiration rate (r'). Points are numbered consecutively from May to September for each station. The points are identified as station B, 1972–77 (1–5); N, 1972–77 (6–10); B, 1978–82 (11–15); N, 1978–82 (16–20); HB, all years (21–25); GL, all years (26–30); and C, all years (31–35).

There was a distinct gradient in ε_w from upper to lower bay. Sources of ε_w were the water itself, dissolved nonchlorophyll colouring substances, and nonalgal particulate matter. Sediment resuspension in the shallow, well-mixed, upper bay may have contributed to high and variable ε_w. In addition, the high river flow in the spring may have increased ε_w throughout the bay and may account for the higher light extinction in the lower bay in May (Millard and Johnson 1986). The underwater light climate can be greatly influenced by ε_w making it an environmental property as important as radiation, temperature, or nutrient supply (Bannister 1974).

In the Bay of Quinte, the underwater light climate was potentially limiting to net photosynthesis at times during the season. However, the relative importance of ε_{PAR} and Z_m to the underwater light climate differed from upper to lower bay. In the extreme lower bay (station C), deep Z_m in May and September may have limited phytoplankton growth. In July and August the shortening of Z_m was a critical factor for algal growth in the lower bay. Here, mixing depth was probably a more important factor than nutrients in controlling phytoplankton growth over most of the season. Algal standing crops in the lower bay were not limited by phosphorus until midsummer when water column stability (N^2) increased and Z_m was shallower (Millard 1986).

Although low values for q_c indicated growth-limiting conditions in the lower bay in September, Chl *a* often remained at July–August levels well into September in spite of deeper mixing depths (Millard and Johnson 1986; Nicholls et al. 1986). There are several explanations for this apparent paradox. Variables used in the critical depth model were long-term averages. As a result, the predictive value of the model for any particular year was limited. Changes in standing crop would have to be related to short-term changes in q_c to demonstrate cause and effect (Jewson 1976). The value in the approach used here was to compare the seasonal and spatial potential importance of changes in key factors such as mixing depth.

Effective mixing depths may not always have been as deep in the lower bay as the weekly estimates indicated, particularly in spring and fall when temperature profiles were quite uniform. Short-term reduction in Z_m during calm periods may have occurred without changing weekly values. As a result, total biomass could have remained stable if species in the community were adapted to these conditions. Haffner et al. (1980) pointed out that the actual magnitude of Z_m may not be as important as the freqency of changes.

The critical depth model of Talling (1971) was very sensitive to r'. In the Bay of Quinte from July to September when Chl *a* was highest, r' was often lower than the estimated seasonal average of 0.11. Standing crops remained high in September when deep Z_m and lower [L.D.H.] meant that r' had to be less than 0.075 for growth to occur. This suggests that the community adapted to the constraints placed on growth by the environment. This process probably occurred via two mechanisms. Some populations present in summer may have had lower respiration rates in response to lower September temperatures (Talling 1957a; Gibson 1975; Minns and Johnson 1986). On the other hand, rapid environmental change may limit the ability of species to adapt physiologically and the community adapts through species succession (Haffner et al. 1980; Harris et al. 1980). In the lower bay, phytoplankton communities were constantly adapting to the frequent changes that occurred in water column stability caused by both wind and intrusions of Lake Ontario water (Freeman and Prinsenberg 1986). The fluctuating and diverse phytoplankton community in the lower bay (Nicholls et al. 1986) was a product of this variable environment similar to the situation found in Hamilton Harbor, Lake Ontario (Haffner et al. 1980). Although average levels of Chl *a* were often similar in summer and early fall, changes in species composition indicated that the community responded to the changing light climate. Certain species such as *Stephanodiscus astraea* (Ehr.) Grun. and *Oscillatoria aghardi* Gom. appeared in the fall assemblage (K.H. Nicholls, unpubl. data). These species often flourish under optically deep conditions (Haffner 1977; Haffner et al 1980; Reynolds 1984). Harris (1978) pointed out that species growing in deeply mixed columns often exhibit some of the lowest values for r'. He suggested that the physiological properties of these species match the requirements of the environment. Heavy diatoms such as *Melosira* spp. and *Stephanodiscus* spp. that are abundant in the spring, but disappear in the lower bay as Z_m shortens in summer, also became more abundant in the fall. In most years, standing crops did decline by late September or early October, suggesting either a lag in response to deeper Z_m or the effect that lower temperatures may have on $P_{\max}$ or a combined effect of these factors.

Prior to phosphorus control in the upper bay the underwater light climate in the summer was limiting for net photosynthesis due to increased $\varepsilon_{\mathrm{PAR}}$ and not Z_m as in the lower bay. Changes in $\varepsilon_{\mathrm{PAR}}$ were due mostly to development of dense algal standing crops. The limitation of net photosynthesis at high standing crops and ΣB levels close to the theoretical maximum ($\Sigma B_{\max}$) suggests that crop development was in equilibrium with the light extinction properties of the water and phytoplankton community. Since Z_m was essentially constant and summer values of [L.D.H.] were not usually limiting, the critical depth equation can be rearranged so that for any r' there was a critical $\varepsilon_{\mathrm{PAR}}$ that defined an upper limit to standing crop set by the light climate. At an average summer [L.D.H.] of 42, a Z_m of 5.0 m, and an r' of 0.075 for the upper bay, the critical $\varepsilon_{\mathrm{PAR}}$ was $3.23 \cdot \mathrm{m}^{-1}$. This was equivalent to 100 mg Chl $a \cdot \mathrm{m}^{-3}$ using the average values for ε_w and ε_s in the upper bay of $0.92 \cdot \mathrm{m}^{-1}$ and 0.023 ln units · mg Chl $a^{-1} \cdot \mathrm{m}^{-2}$, respectively. On 12 occasions, all in the pre-phosphorus control period, $\varepsilon_{\mathrm{PAR}} > 3.00 \cdot \mathrm{m}^{-1}$ was measured. However, the average Chl *a* for these times was only $54\ \mathrm{mg} \cdot \mathrm{m}^{-3}$. Factors such as an increase in ε_w or ε_s or poor extraction of Chl *a* (1972–76) may have been important. On the other hand, there were four occasions when Chl *a* was greater than $100\ \mathrm{mg} \cdot \mathrm{m}^{-3}$ and several others over $80\ \mathrm{mg} \cdot \mathrm{m}^{-3}$. If r' were 0.10, the lower estimates of critical $\varepsilon_{\mathrm{PAR}}$ ($2.43 \cdot \mathrm{m}^{-1}$) and Chl *a* ($66\ \mathrm{mg} \cdot \mathrm{m}^{-3}$) were observed much more frequently and almost entirely prior to phosphorus control. This suggests that prior to phosphorus control, peaks in algal standing crop in the upper bay tended to be light limited. This situation arose because of the high phosphorus supply but was also dependent on algal respiration rates. However, peak standing crops were dominated by *Melosira granulata* (Ehr.) Ralfs and were subject to extreme fluctuations (Nicholls et al. 1986). This heavy diatom requires constant turbulence to remain in the water column and may have suffered high sedimentation losses during calm periods, thus accounting for the high variability in weekly biomass (Lund 1954, 1955).

Prior to phosphorus control, high phosphorus supply and low summer flow (Millard and Johnson 1986; Minns et al 1986) made the upper bay a nutrient-saturated environment where nutrient limitation of phytoplankton growth was unlikely. Limits to size of euphotic zone standing crops and integral primary production were determined by background light extinction, self-shading properties, and photosynthetic capacity of the community as well as biomass loss factors. In the lower bay, it is likely that the mixing regime has always been the factor most controlling to algal growth.

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References

BANNISTER, T. T. 1974. Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnol. Oceanogr. 19: 1–12.

BINDLOSS, M. E. 1974. Primary productivity of phytoplankton in Loch Leven, Kinross. Proc. R. Soc. Edinb. Sect. B (Biol. Sci.) 74: 157–181.

1976. The light climate of Loch Leven, a shallow Scottish lake, in relation to primary production by phytoplankton. Freshwater Biol. 6: 501–518.

CURL, H., AND L. F. SMALL. 1965. Variations in photosynthetic assimilation ratios in natural marine phytoplankton communities. Limnol. Oceanogr. 10 (Suppl.): R67–73.

Environment Canada. 1979. Analytical methods manual. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

Falkowski, P. G. 1981. Light–shade adaption and assimilation numbers. J. Plankton Res. 3: 203–216.

Field, S. D., and S. W. Effler. 1983. Light attenuation in Onondaga Lake, NY, U.S.A., 1978. Arch. Hydrobiol. 98: 409–421.

Freeman, N. G., and S. J. Prinsenberg. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Can. Fish. Aquat. Sci. 86: 270 p.

Ganf, G. G. 1974. Incident solar irradiance and underwater light penetration as factors controlling the chlorophyll *a* content of a shallow equatorial lake (Lake George, Uganda). J. Ecol. 62: 593–610.

Gibson, C. E. 1975. A field and laboratory study of oxygen uptake by planktonic blue-green algae. J. Ecol. 63: 867–880.

Glooschenko, W. A., and H. Curl. 1971. Influence of nutrient enrichment on photosynthesis and assimilation ratios in natural north Pacific phytoplankton communities. J. Fish. Res. Board Can. 28: 790–793.

Glooschenko, W. A., J. E. Moore, M. Munawar, and R. A. Vollenweider. 1974. Primary production in Lakes Ontario and Erie: a comparative study. J. Fish. Res. Board Can. 31: 253–263.

Haffner, G. D. 1977. The production ecology of *Stephanodiscus astraea* (Ehremb.) Grun. Hydrobiologia 54: 247–255.

Haffner, G. D., G. P. Harris, and M. K. Jarai. 1980. Physical variability and phytoplankton communities III. Vertical structure in phytoplankton populations. Arch. Hydrobiol. 89(3): 363–381.

Harris, G. P. 1978. Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. Arch. Hydrobiol. Beih. Ergebn. Limnol. 10: 1–171.

1983. Mixed layer physics and phytoplankton populations: studies in equilibrium and non-equilibrium ecology. Prog. Phycol. Res. 2: 1–52.

Harris, G. P., G. D. Haffner, and B. B. Piccinin. 1980. Physical variability and phytoplankton communities, II. Primary productivity by phytoplankton in a physically variable environment. Arch. Hydrobiol. 88: 393–425.

Harris, G. P., and B. B. Piccinin. 1977. Photosynthesis by natural phytoplankton populations. Arch. Hydrobiol. 80: 405–457.

Jewson, D. H. 1976. The interaction of components controlling net phytoplankton photosynthesis in a well-mixed lake (Lough Neagh, Northern Ireland). Freshwater Biol. 6: 551–576.

1977. Light penetration in relation to phytoplankton content of the euphotic zone of Lough Neagh, N. Ireland. Oikos 28: 74–83.

Jones, R. I. 1977. Factors controlling phytoplankton production and succession in a highly eutrophic lake (Kinnego Bay, Lough Neagh). II. Phytoplankton production and its chief determinants. J. Ecol. 65: 561–577.

Kirk, J. T. O. 1975a. A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. I. General treatment of suspensions of pigmented cells. New Phytol. 75: 11–20.

1975b. A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. II. Spherical cells. New Phytol. 75: 21–36.

Lund, J. W. G. 1954. The seasonal cycle of the plankton diatom *Melosira italica* subsp. subarctica O. Mull. J. Ecol. 42: 151–179.

1955. Further observations on the seasonal cycle of *Melosira italica* (Ehr.) Kutz subsp. subarctica O. Mull. J. Ecol. 43: 91–102.

Millard, E. S. 1986. Seasonal trends in turnover times of orthophosphate in the Bay of Quinte, Lake Ontario, p. 91–99. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Millard, E. S., and M. G. Johnson. 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Ministry of the Environment. 1981. Outlines of analytical methods. Laboratory Services Branch, Rexdale, Ont. 246 p.

Minns, C. K., and M. G. Johnson. 1986. Temperature and oxygen conditions and oxygen depletion in the Bay of Quinte, Lake Ontario, p. 40–49. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H., L. Heintsch, E. C. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Phillips, O. M. 1966. The dynamics of the upper ocean. Cambridge University Press, Cambridge.

Reynolds, C. S. 1984. Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshwater Biol. 14: 111–142.

Reynolds, C. S., and S. W. Wiseman. 1982. Sinking losses of phytoplankton in closed limnetic systems. J. Plankton Res. 4: 489–522.

Reynolds, C. S., S. W. Wiseman, and M. S. O. Clarke. 1984. Growth- and loss-rate responses of phytoplankton to intermittent artificial mixing and their potential application to the control of planktonic algal biomass. J. Appl. Ecol. 21: 11–39.

Robarts, R. D. 1979. Underwater light penetration, chlorophyll *a* and primary production in a tropical African lake (Lake McIlwaine, Rhodesia). Arch. Hydrobiol. 86: 423–444.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. Limnol. Oceanogr. 1: 61–70.

Smithsonian Institution. 1951. Smithsonian meteorological tables. 6th ed. Smithsonian Institution, Washington, DC.

Talling, J. F. 1957a. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. New Phytol. 56: 29–50.

1957b. The phytoplankton population as a compound photosynthetic system. New Phytol. 56: 133–149.

1960. Shelf-shading effects in natural populations of a planktonic diatom. Wetter Leben. 12: 235–242.

1965. The photosynthetic activity of phytoplankton in East African lakes. Int. Rev. Gesamten. Hydrobiol. 50: 1–32.

1971. The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitt. Int. Ver. Limnol. 19: 214–243.

Vollenweider, R. A. 1974. A manual on methods for measuring primary production in aquatic environments. IBP Handb. No. 12. Blackwell Scientific Publications, Oxford. 213 p.

Nitrogen and Phosphorus Limitation to Phytoplankton in the Bay of Quinte and Implications for Phosphorus Loading Controls

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Nicholls, K. H., and E. C. Carney. 1986. Nitrogen and phosphorus limitation to phytoplankton in the Bay of Quinte and implications for phosphorus loading controls, p. 139–144. *In* C.K. Minns, D.A. Hurley, and K.H. Nicholls [ed.]. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nutrient addition experiments with the green alga *Monoraphidium griffithii* during August 1975 demonstrated that nitrogen was limiting to phytoplankton growth in the highly eutrophic upper Bay of Quinte and that phosphorus was limiting in the mesotrophic lower Bay of Quinte near Lake Ontario. The total and inorganic N/P ratios existing at the time were also in agreement with generally accepted values indicative of N limitation in the upper bay and P limitation in the lower bay. Periods of likely N limitation were shown to be much less frequent after implementation of a programme to reduce P loading to the Bay of Quinte and coincided with a marked reduction in biomass of N-fixing planktonic algae. A simple model illustrating the effects of point source P loading reductions in N-limited waters was developed. It is important that lake management personnel understand that N limitation is a feature of highly eutrophied waters enriched by excessive P loading and that P loading control can be as effective in these situations as in P- limited systems.

Des expériences sur l'apport de bioéléments avec l'algue verte *Monoraphidium griffithii* menées en août 1975 ont révélé que l'azote limitait la croissance phytoplanctonique dans la partie supérieure de la baie de Quinte, fortement eutrophe, et que le phosphore était limitatif dans la partie inférieure mésotrophe de la baie, près du lac Ontario. Les rapports entre N et P total et inorganique à ce moment-là concordaient aussi avec les valeurs généralement acceptées indicatrices d'une restriction liée à N dans la baie supérieure et à P dans la baie inférieure. On a démontré que les périodes de restriction possible liée à N sont beaucoup moins fréquentes depuis la réalisation d'un programme visant à réduire la charge de phosphore dans la baie de Quinte et qu'elles coïncidaient avec une baisse marquée de la biomasse d'algues planctoniques fixatrices de N. On a élaboré un modèle simple concernant les effets de la réduction de la charge de P à la source ponctuelle sur des eaux limitées par N. Il est important que le personnel responsable de la gestion de lacs comprenne que la restriction liée à l'azote est une caractéristique des eaux fortement eutrophes enrichis par une charge excessive de phosphore et que le contrôle de la charge de phosphore peut être aussi efficace dans ces situations que dans des systèmes limités par le phosphore.

Introduction

Control of algal growth by N limitation at certain times of the year may be a common feature of eutrophic lakes (Nicholls 1976; Forsberg et al. 1978; Schelske et al. 1978; Horne 1979). In the Bay of Quinte, summer concentrations of nitrate were often undetectable (<10 μg N/L) during the early 1970's (Robinson 1986). Since the implementation of a programme to reduce municipal loadings of P to the Bay of Quinte from sewage treatment plants (Minns et al. 1986) there have been increases in summer levels of inorganic N in the Bay of Quinte (Robinson 1986), which Nicholls et al. (1986) attributed to decreased utilization by phytoplankton.

Since Millard (1986) suggested that phytoplankton growth in the Bay of Quinte was P limited after P loading controls were implemented, the question of nutrient limitation prior to 1978 is especially important because there have been suggestions that P loading controls may not be effective in waters where algae growth is limited by N (Horne 1979; Vincent 1981).

This study reports on bioassays done during 1975 to determine the relative importance of N and P as limiting nutrients in the upper, highly eutrophic and lower mesotrophic Bay of Quinte of Lake Ontario, prior to major reductions in P loading.

Methods

Sample collections at station B (near Belleville in the upper Bay of Quinte) and at station C (Conway, near Lake Ontario) and analyses of nutrients and phytoplankton have been described by Robinson (1986) and Nicholls et al. (1986).

For the algal assay, euphotic zone samples were collected on August 11 at station B and August 12 at station C in 1975, stored in the dark on ice, and returned to Toronto on August 14. The samples were sterilized by slow filtration (0.5 atm (50.7 kPa)) through prewashed Millipore filters of 0.22-μm porosity. Samples were prepared in triplicate for four treatments: a control (no nutrients added), N-spike, P-spike, and N + P-spike. Volumes of media and nutrient spikes were adjusted with sterile distilled water to yield final volumes of 100 mL:

	Volume (mL)			
	Control	N-spike	P-spike	N + P-spike
Sample	97	97	97	97
Distilled water	2	1	1	0
N solution	0	1	0	1
P solution	0	0	1	1
Inoculum *(Monoraphidium)*	1	1	1	1
Total	100	100	100	100

Nitrogen and phosphorus spikes were added as solutions of KH_2PO_4 and $NaNO_3$ to yield additions of 1125 μg N/L and 50 μg P/L to the final media.

We selected *Monoraphidium griffithii* (Berkel) Kom-Legn. as the test organism, since a healthy stock culture had been maintained in our laboratory for several months in P.A.A.P. medium

TABLE 1. Chemical composition (N, P, Na, and K, mg/L) of the algal assay media prepared in triplicate from filtered samples collected at the Belleville and Conway locations, August 11 and 12, 1975. The media were not analyzed, but data are based on results of analyses of additional filtered samples collected at the same time at the Belleville and Conway location, and effects of chemical additions (spikes) are assumed to be directly additive. The total N/P ratios (unfiltered) found at the time were 8.3 and 18 at Belleville and Conway, respectively.

	Belleville				Conway			
	Control	N-spike	P-spike	N + P-spike	Control	N-spike	P-spike	N + P-spike
Dissolved reactive P	0.023	0.023	0.073	0.073	0.006	0.006	0.056	0.056
NO_3^--N	0.005	1.130	0.005	1.130	0.005	1.130	0.005	1.130
NO_2^--N	0.004	0.004	0.004	0.004	0.005	0.005	0.005	0.005
NH_3-N	0.100	0.100	0.100	0.100	0.040	0.040	0.040	0.040
Total inorganic N	0.109	1.234	0.109	1.234	0.050	1.175	0.050	1.175
Na	4.4	6.3	4.4	6.3	11.5	13.4	11.5	13.4
K	0.80	0.80	0.86	0.86	1.0	1.0	1.06	1.06
Inorganic N/P	4.7	53.6	1.5	16.9	8.3	195.8	0.9	21.0
Na/K	5.5	7.9	6.1	7.3	11.5	13.4	10.8	12.6

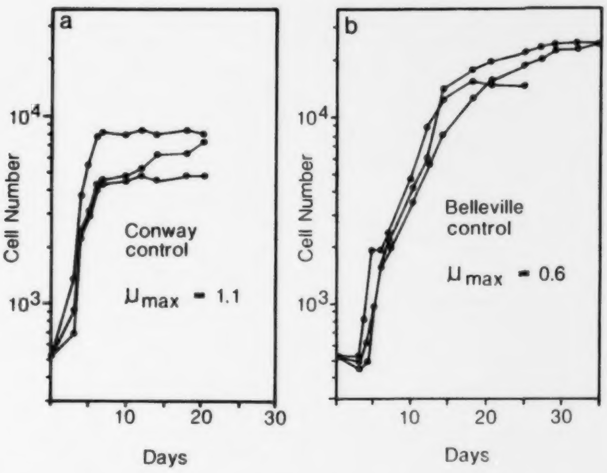

FIG. 1. Growth of the test alga *M. griffithii* in filtered Bay of Quinte water from (a) station C near Lake Ontario and (b) station B in the upper Bay of Quinte.

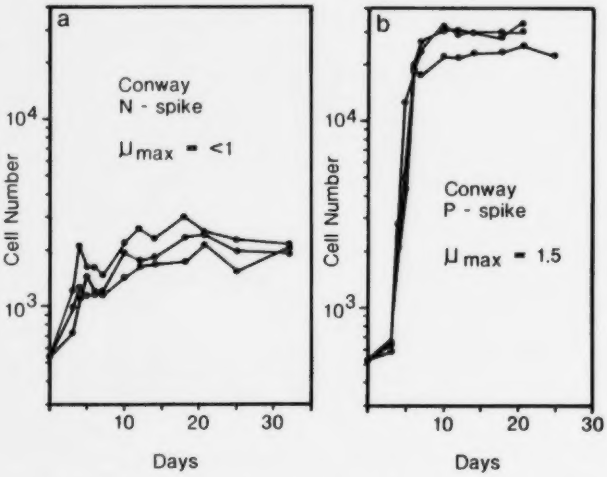

FIG. 2. Growth of the test alga *M. griffithii* in filtered Bay of Quinte water (station C) plus added (a) nitrate and (b) phosphate.

(United States Environmental Protection Agency 1971), and because *M. griffithii* occurred naturally in the Bay of Quinte (Nicholls and Carney 1979).

Cells of a 7-d-old stock culture of *M. griffithii* were washed with sterile 0.5% NaCl solution to remove external nutrients and then rinsed several times with sterile distilled water onto a prewashed 0.45-μm-porosity membrane filter; the filter was then placed in 50 mL of sterile distilled water and mechanically shaken for 1 d to minimize nutrient carry-over effects. The inoculum volume was adjusted so that the initial concentration of cells was about 500/mL for all treatments.

Incubation was in 250-mL sterile flasks at 23°C and continuous illumination was by "cool white" fluorescent lamps providing 4300 lx to the flasks which were anchored on a mechanical shaker reciprocating at 80 strokes/min. The flasks were stoppered with nonabsorbent cotton. Daily counts were performed microscopically on subsamples in a Sedgewick-Rafter counting chamber during the exponential growth phase and every 2–3 d thereafter. Counting was discontinued after 35 d or when there were no longer significant changes in cell number. Algal response to the nutrient additions was assessed as maximum yield, and as maximum specific growth rate (μ_{max}), where

$$\mu = \frac{\ln (X_2/X_1)}{t_2 - t_1}$$

and X_2 = cell number at end of a selected time period (exponential growth phase), X_1 = cell number at beginning of selected time period, and $t_2 - t_1$ = time in days during corresponding interval.

Results and Discussion

The nutrient additions to the filtered Bay of Quinte water resulted in a 3- to 10-fold increase in dissolved reactive P in the P-spiked media, and about a 10- to 20-fold increase in inorganic N in the nitrate-spiked media. Ratios of inorganic N/P ranged from approximately 1 to 200, depending on treatment (spiked or not). However, neither the levels of Na and K nor the ratios of Na/K were altered appreciably (Table 1).

Growth of *Monoraphidium* in the control media (filtered Bay of Quinte water) showed good replicability, and maximum yields of about 7 × 10^3 and 22 × 10^3 cells/mL were achieved

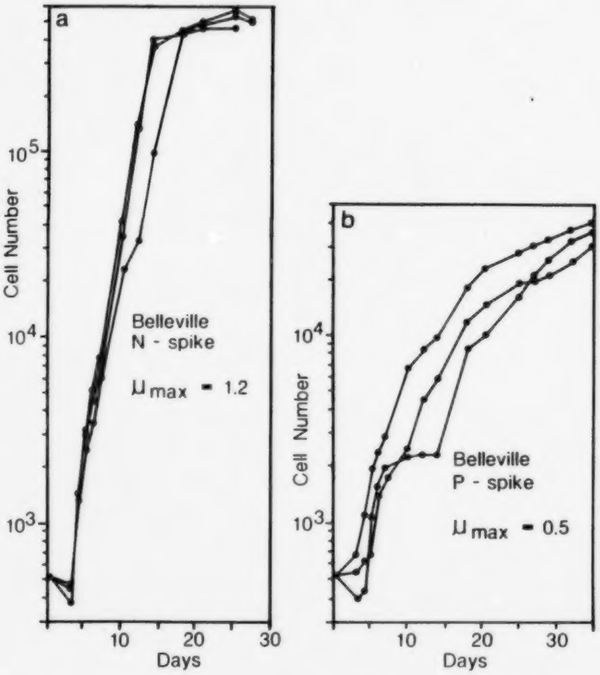

FIG. 3. Growth of the test alga *M. griffithii* in filtered Bay of Quinte water (station B) plus added (a) nitrate and (b) phosphate.

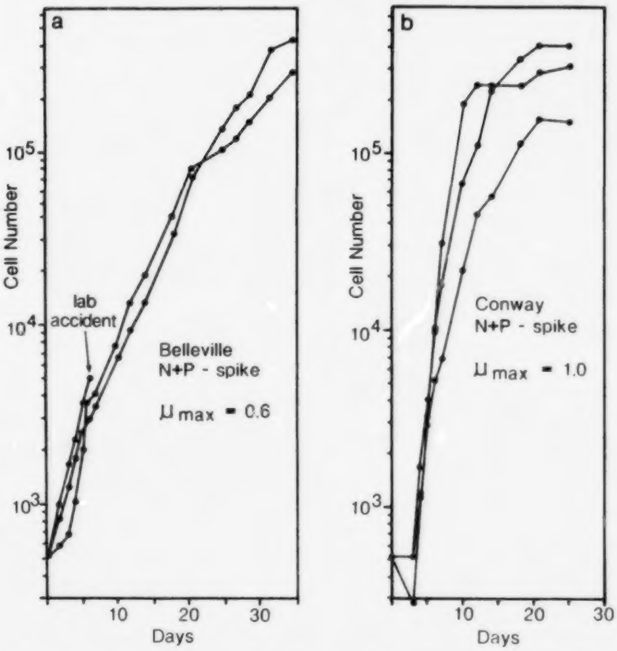

FIG. 4. Growth of the test alga *M. griffithii* in filtered Bay of Quinte water with added nitrate and phosphate from (a) station C and (b) station B.

after about 25 d in water from stations C and B, respectively (Fig. 1):

	Yield$_{max}$ ($\times 10^3$ cells/mL; $\bar{x} \pm 1$ SD)	
	Belleville (B)	Conway (C)
Control	21.9 ± 5.3	7.0 ± 1.8
N-spike	523.3 ± 61.9	2.5 ± 0.4
P-spike	36.2 ± 4.0	29.6 ± 3.7
N + P-spike	355.0 ± 91.9	284.4 ± 120.7

In contrast with the controls, the yields in the N-spiked media from Conway were significantly lower than in the controls, while the P-spiked media from the same site showed yields and μ_{max} values that were significantly higher than the controls (Fig. 2). The μ_{max} of the *Monoraphidium* in the N-spiked medium from Belleville was two times higher than the controls or the P-spiked or the N + P-spiked media from Belleville (Fig. 3 and 4). The maximum yields in the N-spiked Belleville media were also very much higher than the other Belleville media.

Total cell yields in the Belleville media spiked with P alone were not significantly different from those in the control media. Yields in the Conway media with added N + P were significantly higher than with P added alone (compare Fig. 2b and 4b; all tests of significance were based on *t*-tests at $P < 0.05$).

Based on both μ_{max} and yield, the *Monoraphidium* bioassay of filtered Bay of Quinte water clearly shows N limitation at an inorganic N/P ratio of 4.7 in the eutrophic upper Bay of Quinte and P limitation at an inorganic N/P ratio of 8.3 in the mesotrophic lower bay (Table 1). Total N/P ratios (unfiltered) existing at the time in the upper (Belleville) and lower (Conway) Bay of Quinte were 8.3 and 18, respectively. O'Brien (1972) cautioned that changes in growth rate are probably more important than differences in yield when evaluating results from nutrient addition experiments. Less emphasis should be placed on cell yields because, as nutrients are added, one nutrient (or other limiting factor) can replace another as the test organism grows (Zevenboom and Mur 1978). This was most evident in the responses of *Monoraphidium* to N and P additions of filtered Conway water (Fig. 4b). Phosphorus was initially limiting but N became limiting at cell yields of about 3.0×10^4 cells/mL with added P. With both N and P added, yields of 1.5×10^5 to 4×10^5 cells/mL were achieved.

Nutrient enrichment experiments are the most widely used methods for determining nutrient limitation in lakes (Schelske 1984). The usual procedures, using P and N spiking of lake water containing either test organisms or natural phytoplankton assemblages, have been employed so frequently that it is now probably safe to generalize about N or P limitation based on chemical analyses of dissolved and total N and P in lake water. Chiaudani and Vighi (1974), Forsberg et al. (1978), and Vincent (1981) all suggested that N will be limiting if the inorganic N/P ratios are <5–6. Similarly, Rinne and Tarkiainen (1978) and Forsberg et al. (1978) suggested that total N/P ratios <10 imply N limitation and ratios >17 imply P limitation. Clearly, there can be no well-defined or universal distinction between a ratio indicative of N or P limitation in the range 10–17 because it is known that different algal species show different optimum ratios of N and P (Rhee and Gotham 1980). Waters with total N/P ratios in this range may show either N or P limitation depending on the species composition of the phytoplankton and other factors. The N/P ratios existing in the Bay of Quinte at the time of the algal assays during August 1975 are in agreement with those published values (see above) associated with N limitation for the upper bay and P limitation for the lower bay.

It is instructive now to examine differences in the N/P ratios and biomasses of N-fixing algae (*Anabaena* and *Aphanizomenon* spp.) in the upper Bay of Quinte before and after

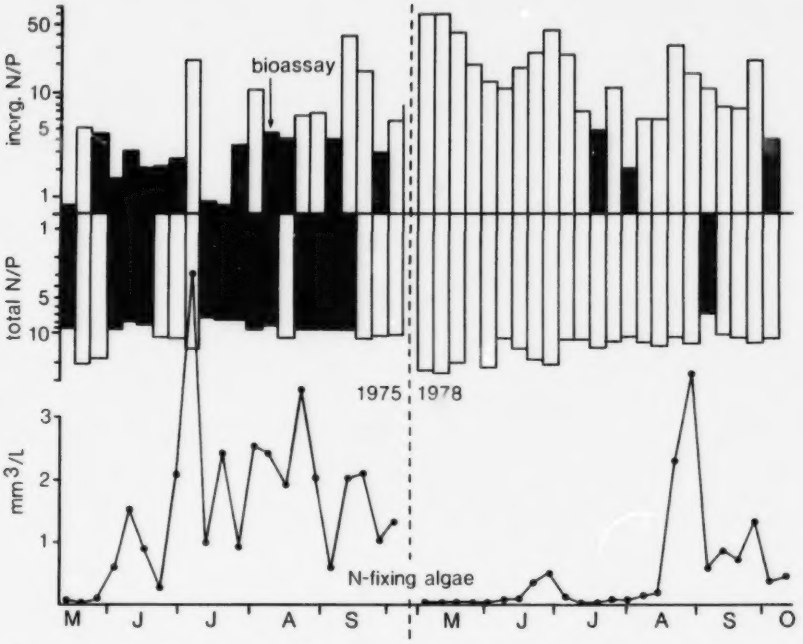

FIG. 5. Total and inorganic N/P ratios and biomass of N-fixing algae (*Anabaena* + *Aphanizomenon* spp.) at station B in the Bay of Quinte during the May–October periods of 1975 and 1978. The blackened portions indicate periods of probable N limitation based on inorganic N/P ratios of <5 and total N/P ratios <10.

reductions in P loading. Data from station B, 1975 (site and year of the algal assays), and station B, 1978, immediately following major reductions in P loading were selected to illustrate the marked decline in N-fixing planktonic algae (Fig. 5). The response at station B was typical of the response at other sampling sites in the upper Bay of Quinte (Nicholls et al. 1986). The decline of N-fixing algae was associated with much less frequent occurrence of N-limited conditions in 1978 compared with 1975 (Fig. 5). During 1975, there were probably very few occasions when N was not limiting. In contrast, at no time during 1978 did measurements of inorganic N/P ratios and total N/P ratios simultaneously suggest N limitation (Fig. 5).

Nitrogen-fixing algae are favoured over other species when inorganic N is limiting (Schindler 1977); their decline, when N/P ratios increase to levels not usually associated with N limitation, is therefore to be expected. However, much of the decline in biomass of N-fixing species in the Bay of Quinte was attributed to the direct effects of P loading controls and lower P concentrations (Nicholls et al. 1986). Some further interpretation of the P reduction effects can be made from the relative abundance of *Anabaena* and *Aphanizomenon* spp. before and after reductions in P loading:

	Anabaena + *Aphanizomenon* spp. (% of total biomass)	
Quinte station	1972–77	1978–81
T	12	19
B	14	17
N	30	36
HB	25	36
GL	15	27
C	13	22

At all six sampling sites, the N-fixing algae constituted a higher proportion of the total phytoplankton after P loading reductions than before. This suggests that the P removal effect on biomass of non-N-fixing algae was greater than the combined effects of P removal and N/P ratio increases on N-fixing algae. Smith (1983) has shown, in a review of world data, that blue-green algae were abundant in lakes with total N/P ratios lower than 29:1. Ratios in the upper Bay of Quinte, after P loading controls were initiated, averaged 14–17 (Robinson 1986). It is likely, therefore, that further reductions in P loading (and the resulting further increases in inorganic N/P ratios) will be necessary to fully exploit the potential for a major shift from N-fixing algae to more desirable species in the Bay of Quinte.

P Loading Reductions and N-Limited Waters

It has been suggested (Horne 1979; Vincent 1981) that P management strategies might be "inappropriately focused" in cases where lake waters are N limited. Therefore, with the implementation of P loading, the change in status from one of predominantly N limitation to one of P limitation in the inner Bay of Quinte has important implications for nutrient management policies.

Clearly, P loading controls are effective in N-limited waters and the reason seems best illustrated by a simple model of N, P, and phytoplankton in a hypothetical N-limited lake (Fig. 6). Some assumptions of the model are (1) algal growth is not influenced by toxicants or other unusual factors, (2) algal growth is N limited as a result of point source inputs with low N/P ratios (i.e. excessive P supplies), (3) internal sources of nutrients are relatively minor compared with external sources, (4) other sources of nutrients are relatively low-concentration, high-volume inputs with higher N/P ratios (>15), (5) the lake has a water residence time that is not excessively long (<10 yr), and (6) other biotic communities are relatively stable (e.g. no drastic year-to-year differences in fish predation and zoo-

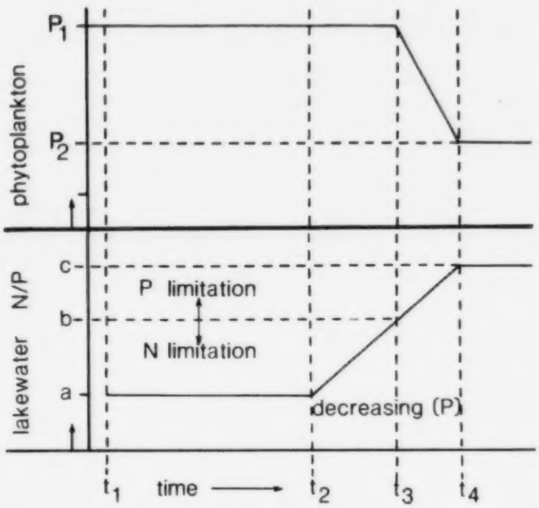

FIG. 6. Model of N, P, and phytoplankton in an N-limited lake (between t_1 and t_3) and under conditions of P limitation (after t_3), subsequent to P loading reductions at t_2.

plankton grazing pressures on phytoplankton).

Over the time interval $t_1 - t_2$, while lake water N/P ratios are within the range associated with N limitation (*a*), phytoplankton densities are held at some average level P_1 (Fig. 6). In this equilibrium state, the phytoplankton is unresponsive to any increases in P concentration. If at t_2, point source P loading is reduced, the phytoplankton is still unresponsive to decreases in P loading until the decreasing P concentrations result (at t_3) in an increase in the lake water N/P ratio above that upper limit (*b*) associated with N limitation (total N/P approximately 10–17). Since the algae are P limited after t_3, further reductions in P loading (and P concentration) will achieve a decrease in production and biomass of phytoplankton until some new steady state is reached (t_4). As well, reductions in P after t_3 will directly cause increases in N/P ratios, and thus may contribute to an alteration of phytoplankton composition (a shift away from N-fixing blue-green algae).

Because the lake and its other inputs act as dilution mechanisms, it may be more reasonable to consider the total reduction in P loading as occurring at t_2, so that the interval $t_2 - t_4$ will be determined by the lake's (or at least its epilimnion) flushing rate and the N/P ratios of its other major sources (direct precipitation, land drainage). It is also important to emphasize that the decrease in phytoplankton (P_1 to P_2) is achieved by decreasing lake water P concentration from t_3 to t_4, not by increasing N/P ratios over the same time interval. A further increase in N/P ratios above *b* is not required to cause a decrease in phytoplankton, but will usually occur because P removal processes in sewage treatment plants are more effective on P than on N. Furthermore, the increase in N/P ratios between t_2 and t_3, leading to a P-limited state, must be achieved by reducing P, not by increasing N. If N loading and N concentration in lake water were increased during $t_2 - t_3$, a P-limited state would be achieved at t_3, but only after increased phytoplankton growth (above P_1), which of course is not desirable, given the objectives of the exercise.

In N-limited lakes where low N/P ratios exist because of excessive P inputs, managers should not dismiss P loading control as an unworkable solution to eutrophication problems. Information about average P levels and N/P ratios in the major sources and in the lake water during the growing season, as well as lake morphometric and hydrologic data, can be used to estimate the P loading reductions required to increase N/P ratios to a level associated with a P-limited state (see Vollenweider and Kerekes (1981)), for formulae relating lake flushing rate, P loading and retention to lake water P concentrations). Further calculations to show P loading reductions required to achieve some measure of trophic state "improvement" can be made from empirical relationships between P concentration, phytoplankton density, and Secchi disc visibility (e.g. Nicholls and Dillon 1978; Canfield and Bachmann 1981).

In the Bay of Quinte, which flushes several times with the annual spring runoff, the rise in N/P ratios through the P limitation threshold (*b* in Fig. 6) must have been achieved very quickly. Major reductions in P loading were achieved between the 1977 and 1978 study periods, so that by the spring of 1978 the bay had already apparently established its new status with respect to N/P ratios and P concentrations. Phosphorus loading reductions to the N-limited upper Bay of Quinte were successful in achieving lower phytoplankton densities because decreased P supplies raised the N/P ratios beyond the N- limitation threshold and established a P-limited state in the upper bay.

Acknowledgements

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References

Canfield, D. E. Jr., and R. W. Bachmann. 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. Can. J. Fish. Aquat. Sci. 38: 414–423.

Chiaudani, G., and M. Vighi. 1974. The N:P ratio and tests with *Selenastrum* to predict eutrophication in lakes. Water Res. 8: 1063–1069.

Forsberg, C., S-O. Ryding, A. Claesson, and Å. Forsberg. 1978. Water chemical analyses and/or algal assay — Sewage effluent and polluted lake water studies. Mitt. Int. Ver. Limnol. 21: 352–363.

Horne, A. J. 1979. Management of lakes containing N_2-fixing blue-green algae. Arch. Hydrobiol. Beih. 13: 133–144.

Millard, E. S. 1986. Seasonal trends in turnover times of orthophosphate in the Bay of Quinte, Lake Ontario, p. 91–99. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.]. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.]. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H. 1976. Nutrient–phytoplankton relationships in the Holland Marsh, Ontario. Ecol. Monogr. 46: 179–199.

Nicholls, K. H., and E. C. Carney. 1979. The taxonomy of the Bay of Quinte phytoplankton and the relative importance of common and rare taxa. Can. J. Bot. 57: 1591–1608.

Nicholls, K. H., and P. J. Dillon. 1978. An evaluation of phosphorus–chlorophyll-phytoplankton relationships for lakes. Int. Revue Gesamten Hydrobiol. 63: 141-154.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.]. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

O'Brien, W. J. 1972. Limiting factors in phytoplankton algae: their meaning and measurements. Science (Wash., DC) 178: 616–617.

Rhee, G-Y., and I. J. Gotham. 1980. Optimum N:P ratios and co-existence of planktonic algae. J. Phycol. 16: 484–489.

Rinne, I., and E. Tarkianen. 1978. Algal tests used to study the chemical factors regulating the growth of planktonic algae in the Helsinki sea area. Mitt. Int. Ver. Limnol. 21: 527–546.

Robinson, G. W. 1986. Water quality in the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.]. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Schelske, C. L. 1984. In situ and natural phytoplankton assemblage bioassays, p. 15–47. *In* L.E. Shubert [ed.] Algae as ecological indicators. Academic Press Inc. (London) Ltd., London.

Schelske, C. L., E. D. Rothman, and M. S. Simmons. 1978. Comparison of bioassay procedures for growth-limiting nutrients in the Laurentian Great Lakes. Mitt. Int. Ver. Limnol. 21: 65–80.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–195.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. Science (Wash., DC) 221: 669–671.

United States Environmental Protection Agency. 1971. Algal assay procedure bottle test. National Eutrophication Research Program, Corvallis, OR.

Vincent, W. F. 1981. Rapid physiological assays for nutrient demand by the plankton. I. Nitrogen. J. Plankton Res. 3: 685–697.

Vollenweider, R. A., and J. J. Kerekes. 1981. Appendix 1. Background and summary results of the OECD cooperative programme on eutrophication. *In* L. L. Janus and R. A. Vollenweider (ed.) Summary Report. The OECD Cooperative Programme on Eutrophication, Canadian Contribution. Scientific Series No. 131, Canada Centre for Inland Waters, Burlington, Ont.

Zevenboom, W., and L. R. Mur. 1978. N-uptake and pigmentation of N-limited chemostat cultures and natural populations of *Oscillatoria agardhii*. Mitt. Int. Ver. Limnol. 21: 261–274.

Some Effects of Phosphorus Loading Reductions on Phytoplankton in the Bay of Quinte, Lake Ontario

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The phytoplankton at several sites within the Bay of Quinte was monitored over the period 1972–81 in relation to several other limnological and hydrobiological investigations comprising "Project Quinte." Prior to 1978, phytoplankton biovolumes (averaging about 12 mm^3/L) and species composition in the upper Bay of Quinte indicated a highly eutrophic status. The equation of the line describing the linear relationship between average May–October total phosphorus concentrations and average phytoplankton biovolumes at all sampling sites was as follows: phytoplankton (mm^3/L) = $0.19 \times$ total P ($\mu g/L$) $- 1.8$ ($n = 69$; $r = 0.90$). Reductions of 50–60% in total phosphorus loading for municipal sources during late 1977 resulted in similar percentage reductions in average May–October phytoplankton densities. The dominant taxa (*Melosira, Stephanodiscus, Anabaena,* and *Aphanizomenon* spp.) have all responded with significantly lower seasonal maxima as well as lower May–October average biomasses. As well, there was a significant shortening of the periods of growth of bloom-forming species. Prior to major reduction in phosphorus loading, the Bay of Quinte could be conveniently divided into upper, middle, and lower sections based on phytoplankton communities. After 1977, the distinction between upper and middle sections was not apparent. The altered phytoplankton communities were potentially more "functional" in supporting the aquatic food chain, and the algal related benefits of less severe odour problems and filter clogging at municipal water treatment facilities also were apparent after 1977.

Le phytoplancton de plusieurs endroits de la baie de Quinte a fait l'objet d'une surveillance de 1972 à 1981, de pair avec d'autres études limnologiques et hydrobiologiques effectuées dans le cadre du « Projet de la baie de Quinte ». Avant 1978, les concentrations volumiques de phytoplancton (en moyenne de 12 mm^3/L) et la composition des espèces de la partie supérieure de la baie indiquaient une forte eutrophisation. L'équation de la courbe décrivant la relation linéaire entre la concentration moyenne du phosphore total entre mai et octobre et le volume biologique moyen du phytoplancton à tous les points de prélèvement était : phytoplancton (mm^3/L) = $0{,}19 \times$ P total ($\mu g/L$) $- 1{,}8$ ($n = 69$, $r = 0{,}90$). Les réductions de 50 à 60 % de la charge en phosphore total en provenance de sources urbaines, obtenues vers la fin de 1977, se sont traduites par des pourcentages de réduction semblables des densités moyennes du phytoplancton entre mai et octobre. Les taxons dominants (*Melosira, Stephanodiscus, Anabaena* et *Aphanizomenon* spp.) ont tous réagi en présentant des maximums saisonniers significativement moins élevés ainsi qu'une biomasse moyenne plus faible entre mai et octobre. On a aussi noté un raccourcissement appréciable des périodes de croissance des espèces envahissantes. Avant les importantes réductions des charges de phosphore, il était pratique de diviser la baie de Quinte en zones supérieure, médiane et inférieure en se basant sur les communautés phytoplanctoniques. Après 1977, la différence entre les zones supérieure et médiane n'était plus évidente. Les communautés phytoplanctoniques modifiées semblaient être plus « fonctionnelles » dans leur rôle de base de la chaîne alimentaire aquatique et l'on a aussi noté, après cette année, certains avantages connexes comme une réduction des mauvaises odeurs et du colmatage des filtres des usines d'épuration causés par les algues.

Introduction

The proliferation of planktonic algae is an important manifestation of nutrient enrichment of lakes. Early experience demonstrated that the major categories of trophic state definition (oligotrophy, mesotrophy, eutrophy) were associated with well-defined ranges of total phytoplankton biomass (Vollenweider 1968). The importance of lake water phosphorus concentration as a factor determining yield of algal pigments has been shown for groups of lakes with wide ranges of phosphorus concentrations (Oglesby 1977; Schindler 1978; Nicholls and Dillon 1978; Canfield and Bachmann 1981; Janus and Vollenweider 1981). Similar relationships between total phytoplankton biomass and total phosphorus concentration are assumed to exist, but have rarely been demonstrated (Nicholls and Dillon 1978; Kalff and Knoechel 1978).

There are also few examples of long-term investigation of phytoplankton composition and biomass within lakes experiencing large increases or decreases in phosphorus loading (Schindler and Fee 1974; Dillon et al. 1978; Edmondson 1979 and earlier papers; Nicholls et al 1980; Olsén and Willèn 1980; Cronberg 1982). This has been an unfortunate omission because the biomass and composition of phytoplankton communities relates directly to several aspects of water use by humans (drinking water supply, aesthetic enjoyment) and aquatic food chain function.

Several of the symptoms of the Bay of Quinte's highly eutrophic state (Johnson and Hurley 1986) are associated with the phytoplankton. As early as 1904, surface accumulations of

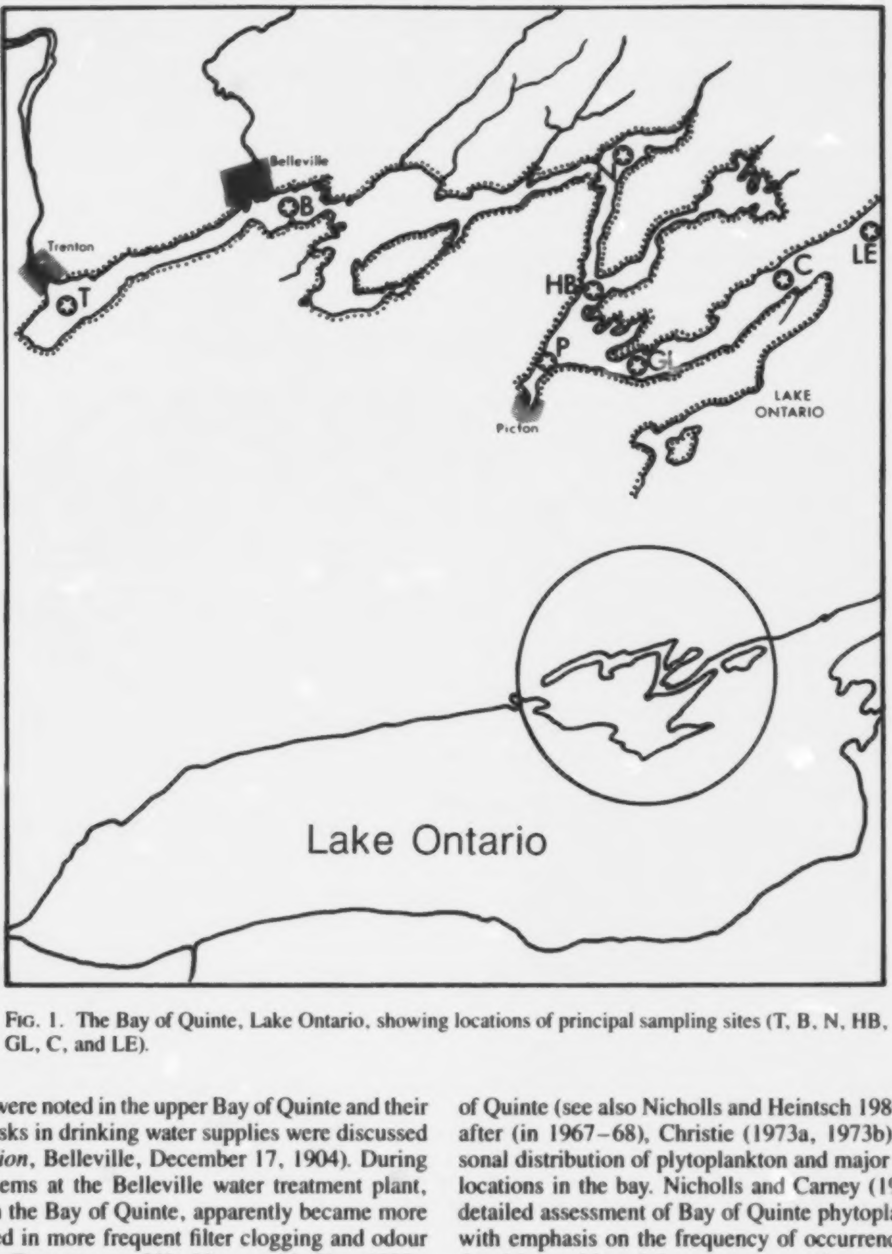

FIG. 1. The Bay of Quinte, Lake Ontario, showing locations of principal sampling sites (T, B, N, HB, GL, C, and LE).

blue-green algae were noted in the upper Bay of Quinte and their potential health risks in drinking water supplies were discussed (*The Daily Ontarion*, Belleville, December 17, 1904). During the 1930's, problems at the Belleville water treatment plant, related to algae in the Bay of Quinte, apparently became more severe and resulted in more frequent filter clogging and odour problems (Ontario Department of Health, unpubl. files, 1938). By 1958, it became necessary to renovate the water treatment operations at the Belleville plant with the addition of four microstrainers ahead of the sand filtration units. Typically, the microstainers were employed for 4–5 mo of every year during the 1950's, 1960's, and early 1970's. During the early 1950's, commercial fishermen in the Bay of Quinte first noticed fouling of their nets by algal "slime" (Hurley and Christie 1977).

The first detailed investigation of phytoplankton in the Bay of Quinte was in 1945 near Lake Ontario (Tucker 1948). This was followed by similar studies by McCombie (1967) who included work in the upper and middle Bay of Quinte for the first time in 1963–64. McCombie (1967) demonstrated a pronounced gradient in trophic state between upper and lower areas of the Bay of Quinte based on phytoplankton density. He also found no conclusive evidence for change since 1945 at the mouth of the Bay of Quinte (see also Nicholls and Heintsch 1986). Shortly thereafter (in 1967–68), Christie (1973a, 1973b) studied the seasonal distribution of plytoplankton and major nutrients at three locations in the bay. Nicholls and Carney (1979) undertook a detailed assessment of Bay of Quinte phytoplankton taxonomy with emphasis on the frequency of occurrence and maximum densities achieved by common and rare taxa during the May–October period of 1975.

The phytoplankton investigation reported in this paper was begun in 1972 as a component of "Project Quinte" (see other papers in this issue). The major objective was to examine the phytoplankton biomass and composition at several sites in the Bay of Quinte over an extended period of several years prior to and following implementation of a phosphorus reduction programme at municipal sewage treatment plants discharging treated effluent. A major reduction was achieved in total phosphorus inputs from municipal sewage treatment plants in late 1977. The municipal "point-source" input averaged 165 kg P/d during 1972–77 and 70 kg P/d during 1978–81 (Minns et al. 1986). An attempt has been made to relate the resulting changes in phytoplankton to the general "suitability" of the Bay of Quinte for human use and aquatic food chain function.

Methods

Phytoplankton samples at each of the eight stations in the Bay of Quinte (Fig. 1) were obtained weekly, May–October, as composites of the euphotic zone by lowering and raising a weighted 1-L bottle with a restricted inlet through a depth corresponding to 2 times the Secchi disc visibility. An assessment of the usefulness of some of the sampling sites led to the deletion of some of the stations part way through the project. The resulting data base for the purposes of this paper is as follows: station T, 1972–80; stations B, N, HB, GL, and C, 1972–81; station P 1972–79; station LE, 1975–77. Station T was sampled in June and August only in 1979 and 1980.

Samples were fixed with glacial acetic acid–Lugol's iodine solution immediately after collection. Cursory examination of the samples in the Toronto laboratory resulted in either a direct subsampling (25 mL, unconcentrated) or a 4–10 times concentration by sedimentation in 100- to 250-mL graduated cylinders for storage in 25-mL screw-capped vials before analysis. All samples collected under the auspices of Project Quinte have been retained in the Ministry of Environment's historical sample repository.

During 1972, the original phytoplankton analyses were made after transferring 1-mL aliquots of the 25-mL stored samples to Sedgewick–Rafter cells; identification and counting were made at 200 × magnification with a compound microscope, and cell density was expressed as areal standard units (ASU). In 1973, a decision was made to express algal densities as cell volumes for the duration of Project Quinte. Consequently, samples collected in 1973 were analyzed with Sedgewick–Rafter cells but density was expressed as cell volume. Approximately 25% of the 1972 samples (about 1/mo at all stations) were reanalyzed with results expressed as cell volume. Analyses since 1973 have been done with inverted microscopes (at 300–600 ×) and Utermohl-type counting chambers.

All samples collected between 1972 and 1979 (inclusive) were analyzed individually; only those from station B during 1980 and 1981 were analyzed individually, while samples from all stations were pooled before analysis in 1980 and 1981. Pooling was done so that a single combined sample representing the entire May–October period was analyzed for each station and yielded a measure of the May–October "average" biomass and composition.

Cell volumes were determined directly from cell measurements and counts. Generally, between 30 and 50 "units" (cells, filaments, colonies) of the taxa contributing most to total biomass were counted and measured. Completed counts totalled 200–500 units and were considered adequate for acceptable precision (Lund et al. 1958; Willèn 1976).

It is apparent that the 1972–73 methods of analysis led to underestimation or nondetection of some very small forms; however, reanalysis of six of the 1973 samples at the higher magnification of the inverted microscope showed increases in total biovolume of only 3–18%, most of which was attributed to counting imprecision rather than to the change of method.

Several people have assisted with analyses over the year of the study (co-authors of this paper). Although this factor has not been addressed specifically with Quinte samples, it has been assessed as part of the regular data quality assurance checks of the Taxonomy Unit and is not considered to have significantly influenced the Project Quinte results. Taxonomic references and procedures have been described in Nicholls and Carney (1979).

Samples of "raw" water for phytoplankton analysis at the Belleville water treatment plant were collected at the low-lift well inside the plant during May–October of 1963–65 and 1970 to the present. Infrequent collections and analyses were also made during other years but are not reported here. Collections were usually made weekly or biweekly, but more frequent collections were made during periods when plant operation was affected by algae. May–October means were unweighted by prior calculation of biweekly or monthly averages.

Analyses of the intake samples followed APHA (1960) using the Sedgewick–Rafter counting chamber and expression of the results as ASU per millilitre, where 1 ASU is equal to 400 μm^2 of an optical cross-sectional area of algal material. The intake was located approximately 0.5 km offshore at 4–5 m water depth; it is approximately 5 km west of Station B (Fig. 1).

Data anlayses include *t*-tests, regression analyses, and analysis of variance with Program No. 406 of Compucorp model 342. Percentage similarities (at the algal class level) were calculated after Nicholls (1985) with a 1:1 weighting of the proportionality and total density factors. Clustering of percentage similarity values as dendrograms followed Sorensen's (1948) method for complete linkage. The method for two-dimensional ordination (polar ordination) is after Bray and Curtis (1957) except that the lengths of the ordination axes were determined by Beals' (1960) formulae after subtraction from the 100% threshold (not Beals' 85% threshold; see also Whittaker 1967).

Results

Dominant Classes and Species

Several important features characterize the Bay of Quinte phytoplankton in the vicinity of Belleville. Most noticeable are the extremely high midsummer densities, especially during the 1972–77 period. Summer maxima greater than 30 mm^3/L at station B and 15 000 ASU/mL in the intake samples were not uncommon (Fig. 2). The instability of these maxima was also apparent; week-to-week changes of 100–300% were frequent (Fig. 2). During the 1972–77 period, microstrainers were routinely in use in the Belleville water treatment plant for most of the ice-free period (4–5 mo).

In both the Belleville intake and the station B samples, similar trends in species dominance were evident. Springtime (May) samples were dominated by ***Stephanodiscus astraea*** (Ehr.) Grun.[1] with lesser quantities of *S. hantzschii* Grun. and *S. invisitatus* Hohn and Hellerman. By midsummer, ***Melosira granulata*** (Ehr.) Ralfs had assumed dominance and was responsible in all years for the recorded maxima. Blue-green algae, of which ***Anabaena spiroides*** Klebahn + var. *crassa* Lemm. and ***Aphanizomenon flos-aquae*** (L.) Ralfs were most important, contributed substantially to total phytoplankton density during the midsummer to fall periods.

Declines in all of these dominant species occurred following phosphorus loading controls in late 1977 resulting in overall reductions in the May–October total phytoplankton densities (Fig. 2). On average, total post-phosphorus control phytoplankton densities were about 50% lower at both station B and in the Belleville intake samples than average pre-phosphorus control values (Fig. 3). Microstrainers in the Belleville plant have been in use for only a few weeks every summer since 1977.

The magnitudes of the average May–October phytoplankton

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[1] *Stephanodiscus astraea* (Ehr.) Grun. has been shown to be an invalid name (Hakansson and Locker 1981). Until a suitable species epithet is determined, we retained the name "*S. astraea*" for the Bay of Quinte population referred to in this paper.

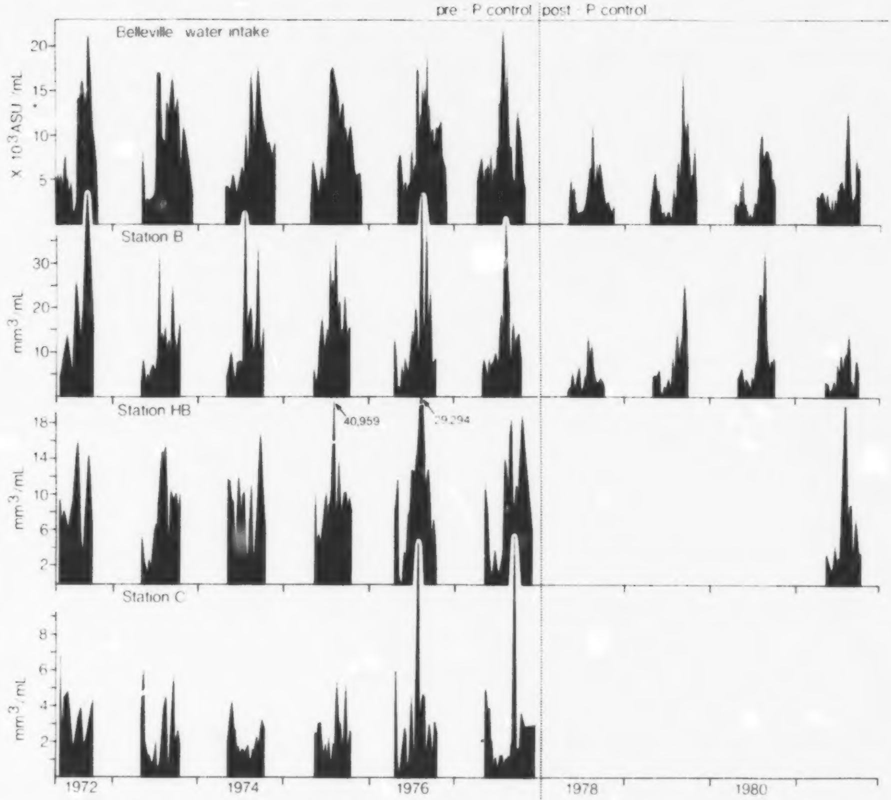

FIG. 2. Total phytoplankton densities measured as areal standard units (ASU) in the raw water of the Belleville water treatment plant and as total cell volume (mm³/L) at other stations in the Bay of Quinte, 1972–81.

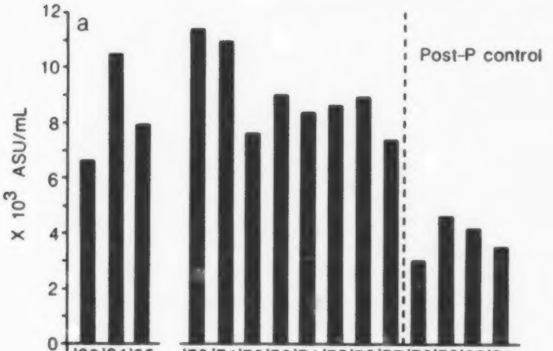

FIG. 3. Average (May–October) densities of total phytoplankton in samples collected (a) through the Belleville water treatment plant intake and (b) at station B in the upper Bay of Quinte.

biomasses have been determined to a large extent by the diatom *Melosira*. The domination of the phytoplankton in the upper Bay of Quinte (station B) by *Melosira* is illustrated by the significant correlation between average May–October biomass and summer maximum *Melosira* (Fig. 4). The smallest *Melosira* maximum recorded since 1972 (11.7 mm³/L) was during August of 1981; the greatest was 41 mm³/L during August of 1976 (Fig. 5). During several years (1973, 1974, 1976, 1977, 1979, 1980) there is some evidence of a spring growth period followed by an early summer decline before the development of the main midsummer population (Fig. 5). In all cases, the summer maxima exceeded spring maxima by about one order of magnitude.

There has been a significant shortening of the periods of substantial growth of several taxa, as well as an overall decline in densities of the dominant species since 1977. For example, the length of the spring growth period of the dominant diatom *S. astraea* has shortened from an average of 10 wk during 1973–77 to an average of 6 wk during 1978–81 (Fig. 6). In all years, densities of *S. astraea* were consistently less than 0.3 mm³/L during August and September (Fig. 5) when *Melosira* was prominent. There is some suggestion that *S. astraea* may be an autumn species, too, because during two years (1974 and 1977), significant peaks were recorded in October (Fig. 5). However, regular sampling into the October–November periods was not done; hence, the consistent occurrence of this phenomenon cannot be confirmed.

The growth periods of the two most important bloom-forming

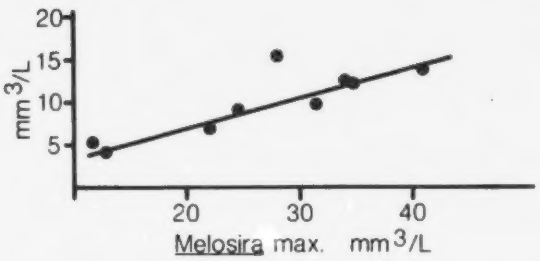

FIG. 4. Relationship between summer maximum *Melosira* and the average May–October total phytoplankton biomass for the years 1973–81 at station B.

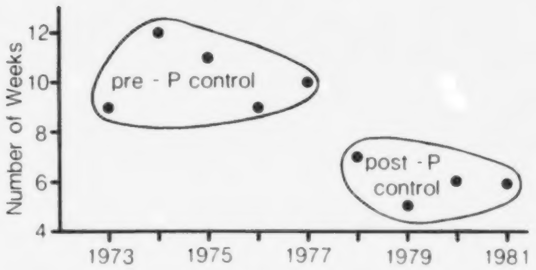

FIG. 6 Length of the spring *S. astraea* growth period (after May 1) at station B before and after implementation of phosphorus loading controls.

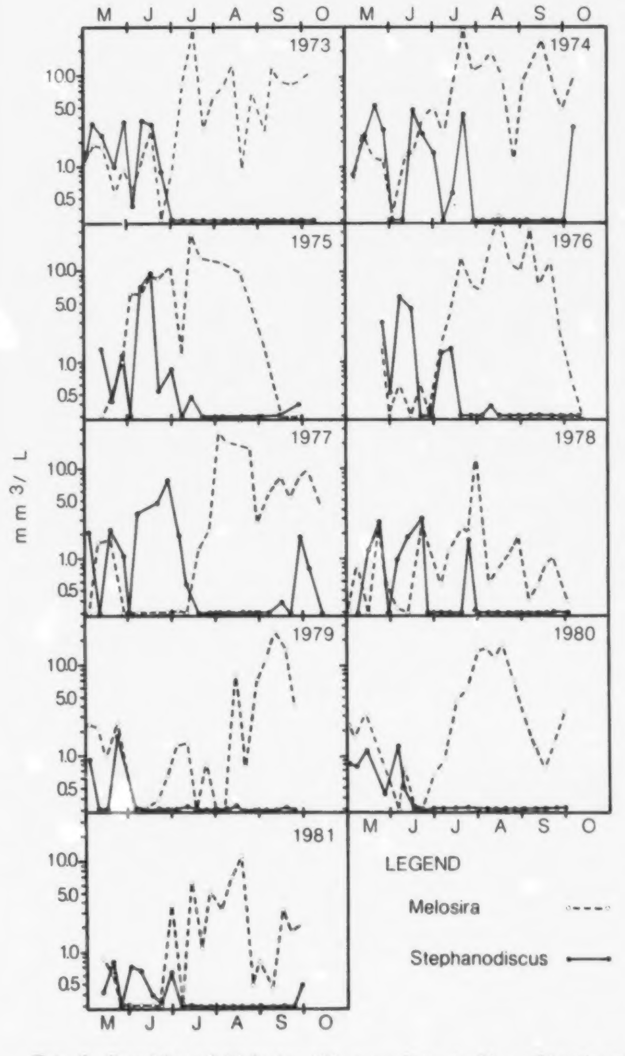

FIG. 5. Densities of *Melosira* (*M. granulata* + *M. ambigua*) and *Stephanodiscus* spp. (mainly *S. astraea*) during May–October of 1973–81 at station B.

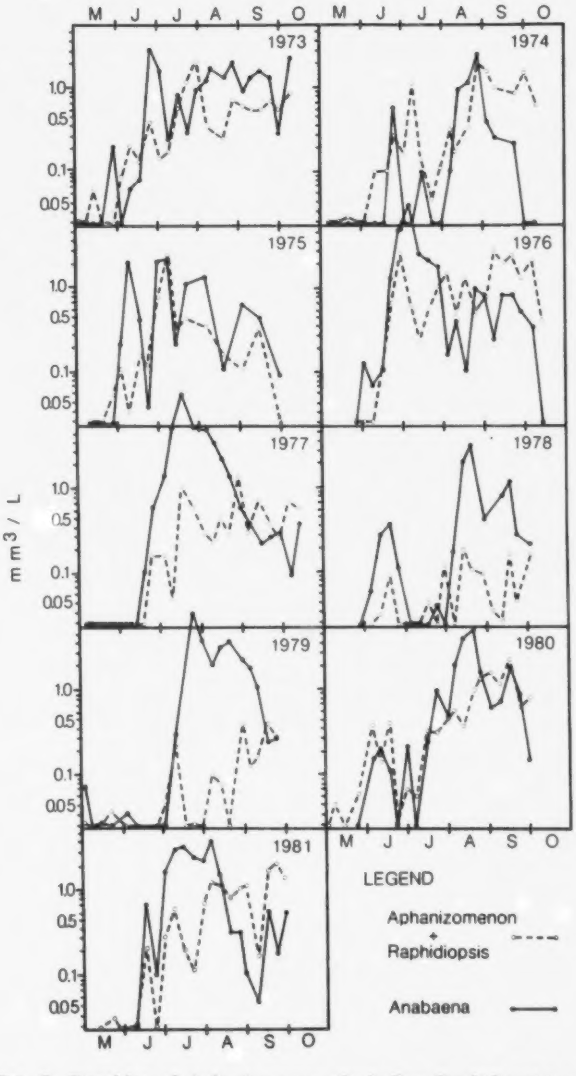

FIG. 7. Densities of *Aphanizomenon* (including *Raphidiopsis*) and *Anabaena* spp. during May–October of 1973–81 at station B.

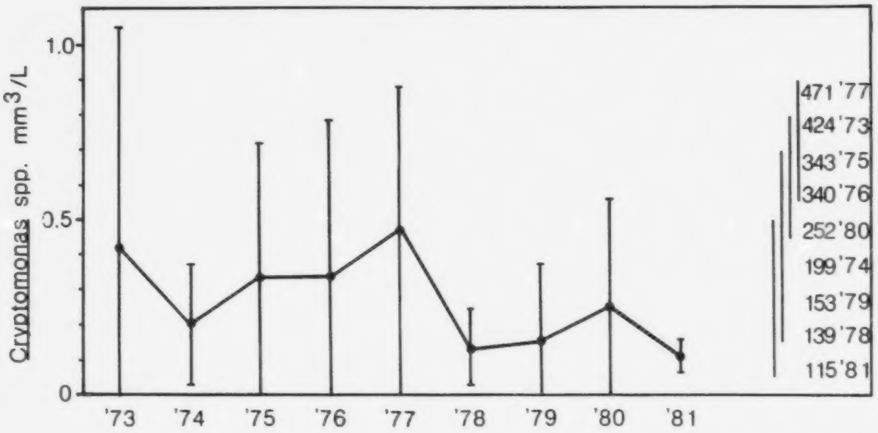

FIG. 8. Average (± SD) of the *Cryptomonas* biovolume at station B during May–October of 1973–81. Mean values at right (mm^3/m^3) are arranged from highest (1977) to lowest (1981) so that values joined by the same line are not significantly different ($P < 0.05$) by analysis of variance and LSD tests.

blue-green algae, *Anabaena* and *Aphanizomenon* (including *Raphidiopsis;* see taxonomic notes in Nicholls and Carney 1979), have shortened since 1977. The number of weeks with *Anabaena* biomass > 0.1 mm³/L was 13 for 1973–77 and 11 for 1978–81. Similarly, the number of weeks with *Aphanizomenon* + *Raphidiopsis* biomass > 0.1 mm³/L was 13 for 1973–77 and 9 for 1978–81. May–October combined average biomasses of these taxa declined from 2.2 mm³/L during 1973–77 to 1.4 mm³/L during 1978–81 at the three upper bay stations, T, B, and N.

Anabaena and *Aphanizomenon* have shown similar seasonal developments; their initial major population increases have generally coincided, although there have been considerable year-to-year differences in the timing. Development of the first major pulse has occurred as early as May (1973) or as late as July (1979), but has usually taken place in June (Fig. 7). The summer maxima of the *Anabaena–Aphanizomenon* complex have been dominated by *Anabaena* during seven years of the 1973–81 period (Fig. 7).

The dominant dinoflagellate was *Diplopsalis acuta* Entz. Unfortunately, this species was not always recognized by all of the laboratory staff and very often it was included with "unidentified Dinophyceae" during phytoplankton enumerations. However, for some years, good records are available and densities exceeding 2 mm³/L were often recorded during 1973–77. Since 1978, *D. acuta* maximum densities have ranged from 0.3 to 1.2 mm³/L. It was typically a mid- to late summer form.

Several species of *Cryptomonas* have been recorded in the Bay of Quinte (Nicholls and Carney 1979) but the dominant is probably *C. erosa* Ehr. Collectively, species of this genus have, on occasion, achieved very high densities. For example, in July of 1973 and 1977, *Cryptomonas* spp. biomasses of 2.8 and 1.2 mm³/L, respectively, were recorded. Densities were lower during the 1978–81 peiod, averaging 0.16 mm³/L compared with a May–October average of 0.36 mm³/L during 1973–77. The 1974 average of 0.20 mm³/L was not significantly different from averages for 1978–81 (Fig. 8).

Major differences in phytoplankton density exist within the Bay of Quinte. There has been a clear gradient from upper to lower bay with densities of algae at station T, B, and N about 5 times higher than at stations C and LE near Lake Ontario (Fig. 9). In most years the uppermost station (T) has shown lower average densities than the other two upper bay stations; only in 1977 was average density at station T greater than at all other sites (Fig. 9). Since 1977, declines of 24–60% in average phytoplankton density have materialized (Fig. 9; Table 1). Prior to phosphorus control in late 1977, the Bay of Quinte could be conveniently divided into upper (T, B, and N), middle (HB and P), and lower (GL and C) sections based on average May–October total phytoplankton densities. After 1977, the distinction between the upper and middle sections was not apparent. There were no significant differences in average biomasses at stations T, B, N, and HB (station P was not sampled) during the 1978–81 period (Fig. 10).

Among the major classes of algae the largest reductions have been in the diatoms (Bacillariophyceae) which comprised 73 and 70%, respectively, of the total phytoplankton biomass at stations T and B during 1972–77, but 61 and 63% during 1978–81. Most of this reduction in diatom representation has been compensated for by increases in representation by blue-green algae (Cyanophyceae). At stations T and B, blue-green algae comprised 17 and 18% of the total during 1972–77, but increased to 26 and 25% during 1978–81. Similar shifts in dominant classes at other Bay of Quinte stations are also apparent (Fig. 9). Notwithstanding the shifts in proportional representation by major classes, it should be emphasized that declines since 1977 in all major classes except the Chrysophyceae are apparent (Table 1).

Because changes in the phytoplankton since phosphorus control in 1977 have involved declines in total densities as well as shifts in the proportionality of major classes, it is useful to relate the 1972–77 and 1978–81 periods to the combined changes in both of these community properties (total density and proportionality of taxonomic content). This was achieved as a two-dimensional ordination (Fig. 11a) such that straight line distances between the points in the ordination field are inversely proportional to calculated similarities (Fig. 11b) giving equal weighting to proportionality of class content and total density (Nicholls 1985). It is apparent that the phytoplankton communities of the upper bay stations T, B, and N (1972–77) are most similar among themselves and least similar to the lower bay stations C and LE (including GL (1978–81)). Of all stations, B and T (1972–77) are most similar. Lower similarities of these stations with N (1972–77) probably relate more to the higher

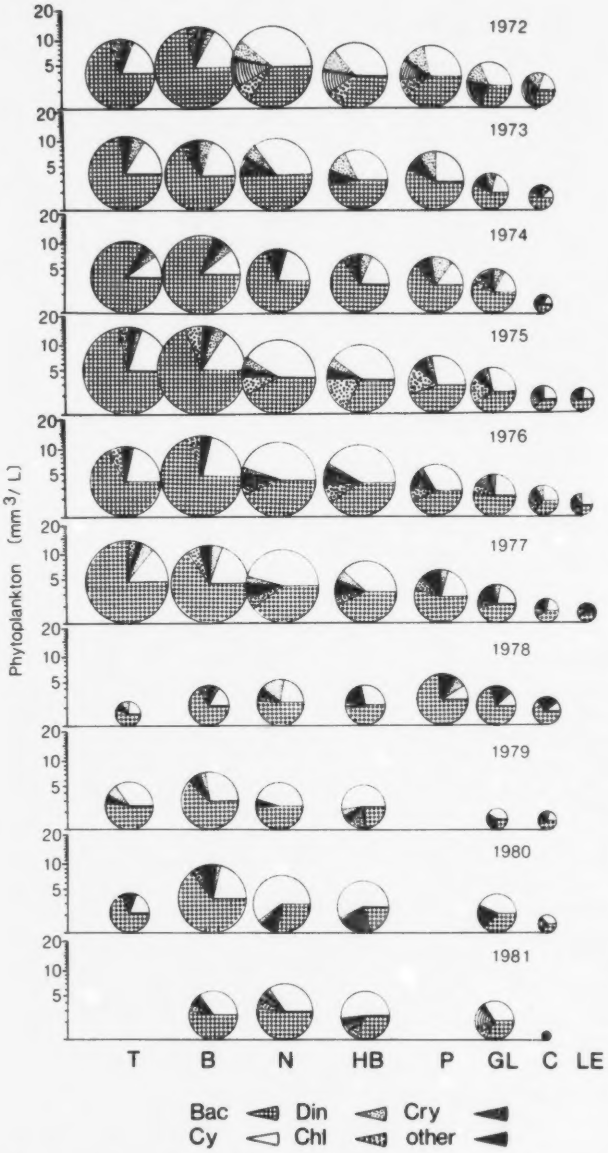

FIG. 9. Average May–October phytoplankton density and class composition, keyed as follows: Bac, Bacillariophyceae; Cy, Cyanophyceae, Din, Dinophyceae; Chl, Chlorophyceae; Cry, Cryptophyceae; others include Euglenophyceae, Chrysophyceae, and Xanthophyceae. The only representative of the Prymnesiophyceae, *Chrysochromulina parva*, was included in the Chrysophyceae for convenience.

proportion of blue-green algae at N (Fig. 9) than to total biomass differences, which are less significant in the calculations of percentage similarity. After phosphorus loading controls in 1977, the upper bay stations, T, B, and N were much more similar to the lower bay stations in ratios of algal classes and total phytoplankton densities. Similar changes are apparent for the middle bay stations HB and GL (Fig. 11a).

Nutrient–Phytoplankton Relationships

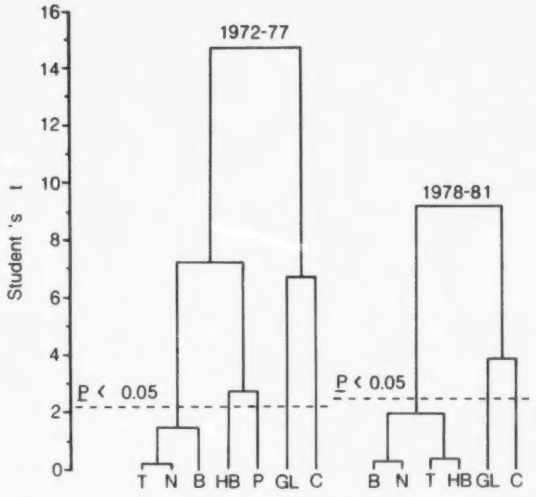

FIG. 10. Dendrograms of Bay of Quinte stations after a clustering of Student's *t* values for all possible pairs of stations based on May–October average phytoplankton biomass during pre- (1972–77) and post-phosphorus (1978–81) control periods. Stations linked at lower Student's *t* values have more similar means than those linked at higher values. Only those stations linked at Student's *t* values less than those indicated by the broken line have mean biomasses which are not significantly different ($P < 0.05$).

A general trend to increasing total phosphorus over the ice-free periods was apparent at upper and middle bay stations (Robinson 1986). At station B, these seasonal trends have not always coincided with the trends in total phytoplankton density, although in some years (e.g. 1975) the trends in phytoplankton closely parallelled total phosphorus (Fig. 12). In 1978, the generally increasing trend in total phosphorus, over the May–October period, was not at all related to total phytoplankton biomass values over the same period. Highest densities of algae were found over a 4-wk period in late July and early August. These were immediately followed by biomass values which were, for several weeks, among the lowest recorded for the summer, despite the presence of the highest total phosphorus values of the summer (Fig. 12). The same seasonal trend in total phosphorus was observed in 1979, but the peaks in phytoplankton occurred in August and September when total phosphorus was also highest. Total phosphorus values during June and July of 1979 were associated with unusually low phytoplankton densities based on total phosphorus to phytoplankton ratios of other years (Fig. 12).

In contrast with total phosphorus, both silica and nitrate nitrogen showed substantial increases since 1977 (Robinson 1986). These trends reflect the reciprocal relationships of these dissolved nutrients with total phytoplankton and diatoms (Fig. 13). The increase in average silica concentration in the inner bay of 3.8 times corresponded with the 66% reduction in diatoms (diatom biomass was 3.0 times greater before 1978).

Anomalies that were apparent with the seasonal distribution of total phosphorus and phytoplankton data were to some extent also found with the silica and diatom data, especially after 1977. Major declines in silica were usually associated with diatom peaks such as occurred during June of 1975, July and August of 1976, and September of 1979 (Fig. 14). However, substantial decreases in silica have occurred which were apparently not associated with significant diatom growth (e.g. May of 1978 and 1979). Another anomalous period was between May and August of 1979 when a consistent increase in silica coincided with increasing diatom biomasses (Fig. 14).

TABLE 1. Average phytoplankton class densities (mm^3/L) at the Bay of Quinte sampling sites over the periods 1972–77 (pre-phosphorus control) and 1978–81 (post-phosphorus control), showing the percentage reduction in the total phytoplankton.[a]

	1972–77								1978–81					
	T	B	N	HB	P	GL	C	LE	T	B	N	HB	GL	C
Cyanophyceae	2.0	2.3	4.4	3.07	1.81	1.09	0.51	0.41	1.2	1.67	2.64	2.5	1.06	0.36
Dinophyceae	0.37	0.47	0.49	0.55	0.54	0.35	0.27	0.12	0.27	0.19	0.33	0.1	0.09	0.02
Cryptophyceae	0.20	0.39	0.67	0.56	0.55	0.47	0.38	0.34	0.14	0.2	0.36	0.56	0.53	0.20
Chrysophyceae	0.07	0.07	0.06	0.09	0.06	0.05	0.04	0.08	0.14	0.08	0.06	0.06	0.04	0.03
Chlorophyceae	0.45	0.62	0.61	0.74	0.55	0.39	0.26	0.27	0.14	0.24	0.23	0.35	0.19	0.11
Bacillariophyceae	8.58	9.25	5.2	3.71	3.56	2.1	1.0	0.81	2.85	4.18	2.77	1.52	1.5	0.78
Total	11.7	13.1	11.5	8.7	7.0	4.5	2.5	2.0	4.7	6.6	6.3	5.1	3.4	1.5
%reduction									60	50	45	41	24	60

[a] Euglenophyceae and Xanthophyceae were negligible and were omitted from this table. All results are arithmetic means of weekly analyses (May–October) except (1) 1972, when samples were analyzed approximately monthly, and (2) during 1978–81, when samples from all stations except B were pooled before analyses. Samples from T were collected during June and September of 1979 and 1980 and were not collected during 1981.

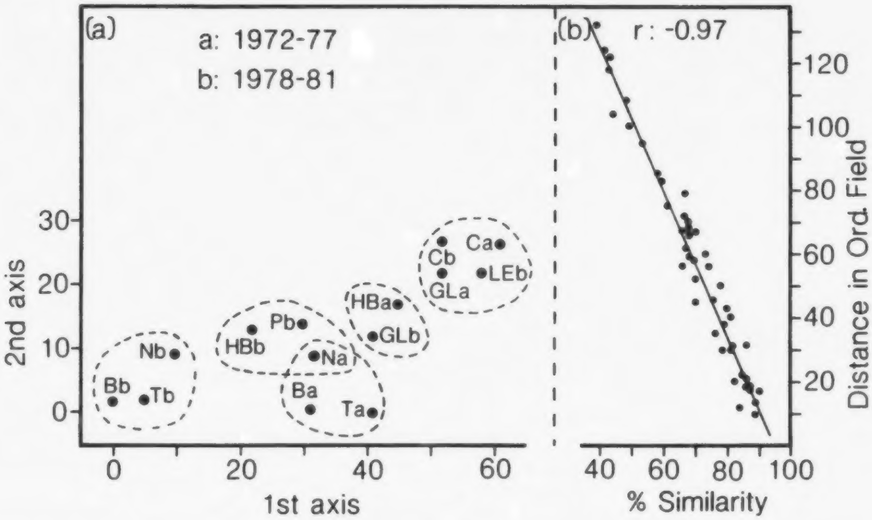

FIG. 11. (a) Two-dimensional ordination of Bay of Quinte sampling stations before and after phosphorus loading reductions ("a" and "b" after a station symbol, e.g. Tb and Ta, refers to "before" and "after"). (b) Regression of straight line distance between pairs of stations in the ordination field on their calculated percentage similarities based on all possible combinations of four randomly selected stations. The highly significant correlation coefficient ($r = -0.97$) meant that a third ordination axis was not needed.

At all Bay of Quinte stations, May–October average total phytoplankton biomass was significantly correlated ($P < 0.001$) with average total phosphorus (Fig. 15). Expressed in predictive terms relevant to changes in phosphorus concentrations, a change of 6 μg P/L was associated with a change in phytoplankton biomass (in the same direction) of 1 mm^3/L.

The responses of the major classes of algae to phosphorus loading controls in the Bay of Quinte have been different. The greatest response has been with the diatoms (Fig. 16) showing a phosphorus to biomass ratio of 7 μm P/mm^3. The blue-green algae had the next highest rate of decrease per unit of phosphorus with a phosphorus to biomass ratio of 20 μg P/mm^3. Response among the other groups has been slight compared with the diatoms and blue-green algae (Fig. 16). The phosphorus to biomass ratio among the sum of the Dinophyceae, Cryptophyceae, Chrysophyceae, Chlorophyceae, and Euglenophyceae was 57 μg P/mm^3.

After phosphorus reductions in 1977, the Chrysophyceae increased (as a percentage of the total phytoplankton biomass) at stations T, B, N, HB, GL, and C, by 5, 2, 4, 1.1, 1.1, and 1.3 times, respectively. This increased representation by Chrysophyceae since 1977 is in agreement with the proportion of the total phytoplankton contributed by this group in other lakes with different or changing phosphorus concentrations (Fig. 17).

Of the major functions and consequences of phytoplankton development in lakes, those influencing the aesthetic appearance and potability of lake water and those influencing food chain function are probably the most relevant elements. The dominant algae implicated in these two roles are those that are toxic, form floating surface accumulations, and are not "food chain functional," and those forms that are relatively small with rapid growth rates and have high nutritional value for planktonic crustacea. More specifically, colonial bloom-forming blue-green algae (*Anabaena*, *Aphanizomenon*, *Raphidiopsis*, *Microcystis*, *Coelosphaerium*, *Lyngbya*, *Oscillatoria*, etc.) comprise the first group, while cryptomonads and chrysomonads probably contribute most to the second group.

A potentially useful index is proposed which expresses the acceptability of the phytoplankton community in terms of its

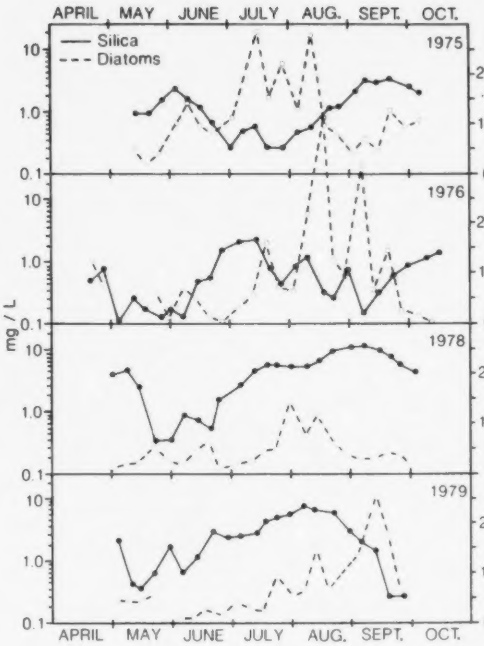

FIG. 12. Seasonal trends in total phosphorus (mg/L) and phytoplankton (mm³/L) during two years immediately before (1975, 1976) and two years immediately after (1978, 1979) phosphorus loading reductions.

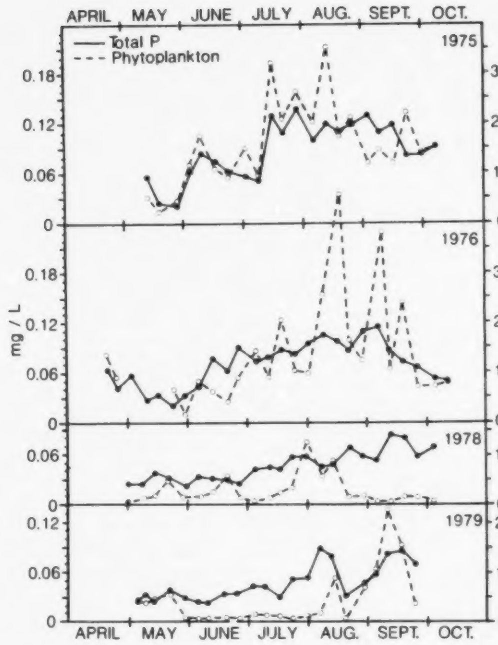

FIG. 14. Seasonal trends in dissolved reactive silicate (mg/L) and diatom biomass (mm³/L) during two years immediately before (1975, 1976) and two years immediately after (1978, 1979) phosphorus loading reductions.

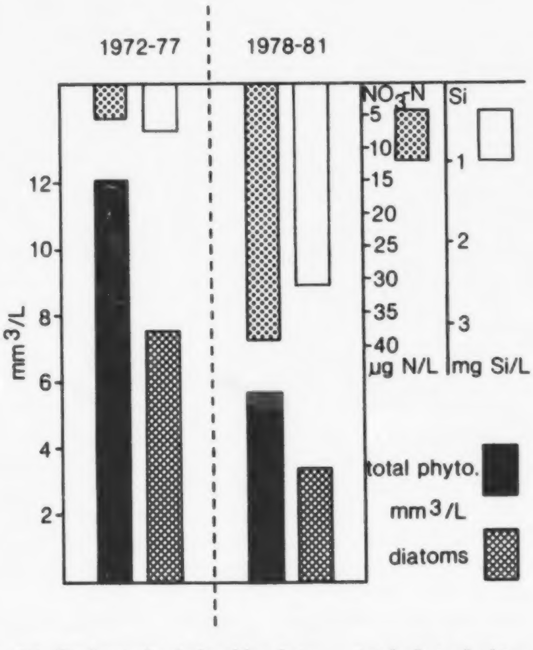

FIG. 13. Reciprocal relationships between total phytoplankton biomass and nitrate-nitrogen and diatom biomass and silica concentrations as average values before and after reductions in phosphorus loading (1972–77 vs. 1978–81).

food chain acceptability and human use aspects. This index, termed the "*F*" value, is simply calculated as the quotient of May–October average biomass of Chrysophyceae + Cryptophyceae divided by average biomass of blue-green bloom formers. Preliminary use of this index suggests that *F* values range over several orders of magnitude in Ontario lakes and are related to average lake water phosphorus concentrations. As an approximate guideline, values >>1 reflect a more "desirable" phytoplankton community than values <<1. In the Bay of Quinte, *F* values have increased since municipal phosphorus loading decreased in 1977 (Fig. 18).

Discussion

May–October average phytoplankton biomasses in the Bay of Quinte are among the highest reported for north temperate eutrophic lakes. Those waters with higher biomasses are small fertilized lakes and ponds or lakes situated in fertile soils and receiving excessive nutrient loads from municipal and/or agricultural sources (Schindler and Comita 1972; Olrik 1973; Schindler et al. 1973; Cook and McComas 1974; Barica 1975; Nicholls 1976a; Coveney et al. 1977; Cronberg 1982). The upper Bay of Quinte, during 1972–77, had higher average phytoplankton biomasses than any other similarly large embayment or open water area of the Laurentian Great Lakes (Munawar and Munawar 1981 and references therein).

Week-to-week fluctuations in total phytoplankton were more closely related to total phosphorus concentrations before phosphorus loading controls than after. This may be because sewage treatment plant effluent after 1977 contained a higher ratio of biologically unavailable phosphorus to available phosphorus; so, a high proportion of the total phosphorus after 1977 at the Bay of Quinte stations was of no immediate use to phytoplankton. Phosphorus in dissolved "reactive" form is usually all readily available for phytoplankton, and Robinson (1986) showed a substantial decrease in dissolved reactive phosphorus after 1977 in the bay. Certainly these relationships will be

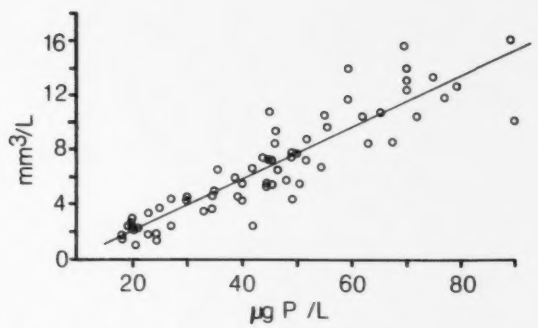

FIG. 15. Relationship between May–October averaging total phosphorus concentrations (µg P/L) and average total phytoplankton density (mm³/L) at Bay of Quinte sampling stations T (1972–80), B, N, HB, GL, and C (1972–81), P (1972–79), and LE (1975–77). The equation is as follows: phytoplankton (mm³/L) = 0.19 × total P (µg/L) – 1.8 (n = 69; r = 0.90).

influenced by short-term or local events, such as sewage treatment plant by-pass during heavy rainfall, and consequent increases in loading of biologically available phosphorus. Summer storms affecting the resuspension of bottom sediment (total phosphorus) and the disruption of diffusion gradients in dissolved phosphorus in the water column (Wright 1976; De Groot 1981) may also influence the short-term total phosphorus to phytoplankton ratios. No attempts to explain all of these short-term (within year) fluctuations in total phosphorus and phytoplankton have been made, but it is clear from the rapid response of May–October average phytoplankton densities that control of phosphorus loading from sewage treatment plants has been effective. Although the municipal point sources contribute only a small proportion of the total phosphorus loading to the bay (Minns et al. 1986), the consequence of these relatively low-flow, high-concentration phosophorus inputs has been dramatically demonstrated by the phytoplankton response after 1977 and is in accordance with earlier predictions (Johnson and Owen 1971).

The decrease after 1977 in phytoplankton biomass followed a clear gradient between the upper bay and Adolphus Reach with reductions of 60, 50, 45, 41, and 24% at sampling stations between Trenton and Glenora. The trend probably indicates the proximity of the sampling stations to point sources of phosphorus and also reflects the magnitude of the phosphorus loading reductions. The Napanee, Hay Bay, and Glenora stations are progressively farther away from major point sources than are the upper bay stations, and the progressively deeper water (greater volume) at these sites further diminished the effect of phosphorus loading reductions.

A 60% decrease in phytoplankton biomass at the Conway station after 1977 destroys the continuity of the trend from upper to lower bay and at first seems anomalous; however, Lake Ontario waters undoubtedly influence the phytoplankton at the Conway site (McCombie 1967; Nicholls and Heintsch 1986) and there have been substantial reductions in phosphorus concentrations in Lake Ontario since 1977 (Dobson 1981).

The major response to phosphorus reductions in the Bay of Quinte was with the diatoms. Concentrations of silica below 150–200 µg Si/L are often associated with declines in diatom populations and, in the presence of adequate levels of other major nutrients, have been found limiting (Lund 1971; Nicholls 1976a; Haffner 1977; LaZerte 1980). Silica levels this low in the Bay of Quinte were never recorded (Robinson 1986), although the influence of seasonal diatom growth on declining silica levels was evident in every year since 1972. Losses other than through diatom sedimentation are probably negligible. The only other major biological sink is the scaled Chrysophyceae (Klaveness and Guillard 1975) which have been poorly represented in the Bay of Quinte. Bailey-Watts (1976) concluded that at certain times of the year, dissolution of sedimented diatom frustules was a more important source of silica than external loading. This is also likely true in the Bay of Quinte where very rapid increases in silica have been observed following major "crashes" of diatom peaks. After reduced phosphorus loading in 1977, the much higher silica levels appear less related to diatom dynamics (much lower diatom densities) and must be related to variations in sources of silica (river inputs, interal regeneration).

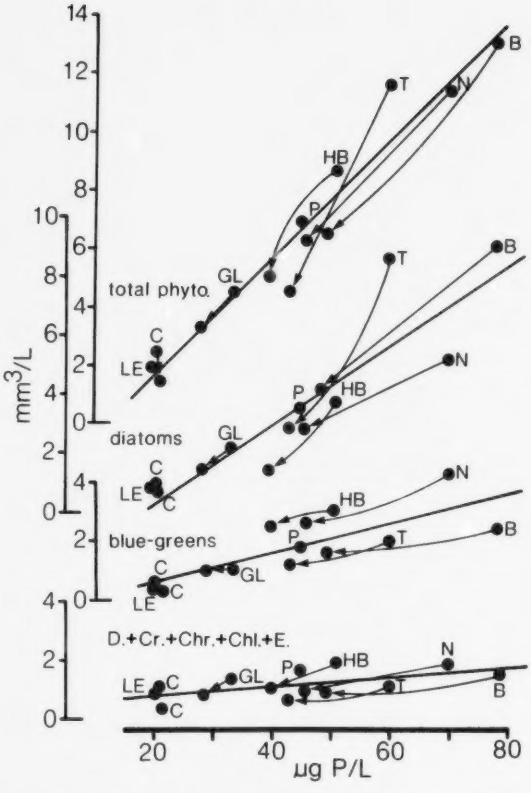

FIG. 16. Regressions of total phytoplankton, diatoms, blue-green algae, and the sum of the Dinophyceae (D.), Cryptophyceae (Cr.), Chrysophyceae (Chr.), Chlorophyceae (Chl.), and Euglenophyceae (E.) on the May–October total phosphorus concentrations during pre- (1972–77) and post-phosphorus (1978–81) control periods (change indicated by arrows). All four relationships are significant at $P < 0.05$, with correlation coefficients of 0.97, 0.90, 0.79, and 0.64, respectively.

It is unlikely that silica alone brought about the decline of the spring *S. astraea* population; silica levels were rarely low enough. Nitrate-nitrogen, on the other hand, had declined to undetectable levels by early summer during most of 1972–77 period. Swale (1963) and Nicholls (1976a) believed that spring *S. hantzschii* populations were limited by inorganic nitrogen.

During 1978, Millard (1986) showed that the greatest demand for phosphorus by algae coincided with the decline of the *S. astraea* population. It is likely then that the spring *S. astraea* was controlled by nitrogen or phosphorus before phosphorus

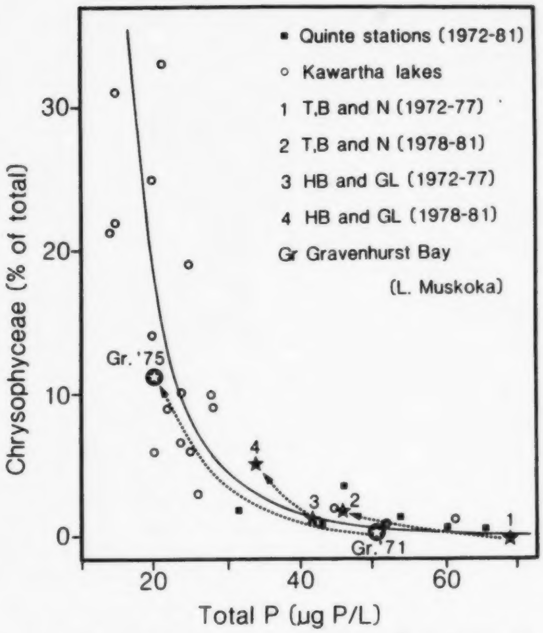

FIG. 17. Density of chrysophycean species as a percentage of total phytoplankton (data for other lakes from Nicholls 1976b).

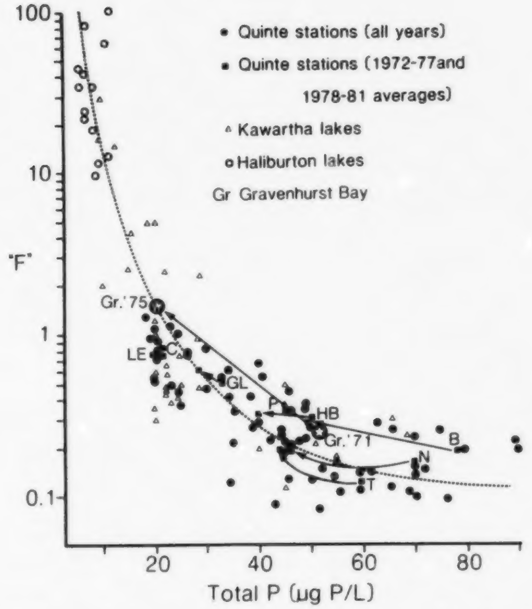

FIG. 18. Relationship between the average May–October total phosphorus concentrations and the *F* index calculated as the sum of the Cryptophyceae and Chrysophyceae, divided by the blue-green bloomer average biomass (data from Kawartha lakes and Gravenhurst Bay from Nicholls 1976b) and Dillon et al. (1978); data from Haliburton lakes unpublished). Arrows indicate changes after phosphorus loading reductions.

loading controls, and by phosphorus after controls if Millard's findings can be assumed to represent the post-phosphorus control period. *Stephanodiscus astraea* is a large and relatively heavy diatom, and as early summer water temperatures increased, the associated increased sinking rates probably also contributed to its loss from the algal community (see also Haffner 1977).

The factor contributing to the decline of the spring *S. astraea* population could not have acted in the same way on *Melosira*, which usually experienced its main increase immediately after the demise of *S. astraea*. Kilham (1971) suggested that the seasonal sequence of planktonic diatoms can be explained by the silica requirements of different species. Based on a literature review, he found that *S. astraea* became dominant at low silica concentrations (0.3 mg Si/L), while *M. granulata* did so at much higher values (6 mg Si/L). He concluded that the high silica diatoms (e.g. *Melosira*) would never replace the low silica diatoms (e.g. *S. astraea*) as levels of silica decreased. In the Bay of Quinte, *Melosira* always replaced *S. astraea* by summer. The role of other nutrients (nitrogen, phosphorus) in Kilham's hypothesis was not evaluated, but later work (Tilman 1977, 1981; Kilham and Tilman 1979) showed that the relative abundances of diatom species were often dependent on the changing ratios of silica to phosphorus and that the results of competition experiments involving two or more species could be predicted from knowledge of nutrient requirements of each species.

In contrast with *S. astraea*, *Melosira* was able to develop high densities in the Bay of Quinte despite scarce amounts of inorganic nitrogen. If inorganic nitrogen levels continue the increase begun after 1977, some changes in seasonal distribution of *S. astraea* and *Melosira* may result. Because silica to phosphorus ratios have dramatically increased since 1977, some further changes may develop in the relative abundance of other diatom species (e.g. *Cyclotella meneghiniana* Kutz., *Fragilaria crotonensis* Kitton) which have been of only minor importance previously.

During August of 1975, inorganic nitrogen levels at station B were shown to be limiting to algal growth (Nicholls and Carney 1986). Summer nitrate-nitrogen concentrations were still frequently at undetectable levels after phosphorus loading reductions in 1977 (Robinson 1986), and nitrogen may still be limiting at certain times, especially in the upper bay.

The decline of nitrogen-fixing algae (*Anabaena* + *Aphanizomenon*) has been proportionately less than of other groups such as diatoms, green algae, or dinoflagellates. This is further evidence for continuing nitrogen limitation, since it is generally accepted that nitrogen-fixing algae are favoured under such conditions (Schindler 1977; Horne 1979). The observed correlation ($r = -0.38$) between biomass of nitrogen-fixing algae and nitrogen to phosphorus ratios throughout the Bay of Quinte, although statistically significant ($P < 0.05$), was less significant than the correlation of nitrogen-fixing algae with total phosphorus ($r = 0.513$). Declines in nitrogen-fixing algae were more likely related directly to lower phosphorus supply than to the increases in inorganic nitrogen. The observed increases in nitrogen to phosphorus ratios since 1977 (Robinson 1986) were probably not great enough to precipitate a major shift away from nitrogen-fixing algae to those forms better able to compete for nutrients and other growth factors in the presence of adequate amounts of dissolved inorganic nitrogen.

It is not clear at this time if such a compositional shift should be anticipated in the near future. Neither is it clear how the changing nutrient ratios will affect *Microcystis*, another particularly offensive blue-green, but non-nitrogen fixing alga in the Bay of Quinte. Lean et al. (1978) found that additions of organic nitrogen to a large (100 m^3) enclosure in the Bay of Quinte stimulated growth of *Microcystis aeruginosa* over nitrogen-fixing species. Horne (1979) suggested that there may be some "irreducible" level of blue-green algae in restored lakes; however, this may depend on final steady-state nitrogen to phosphorus ratios. Smith (1983) reported a markedly lower contribution by blue-green algae in lakes with total nitrogen to phosphorus ratios greater than 29. Experience in Ontario with phosphorus loading controls has demonstrated that the major response of the phytoplankton was with blue-green nitrogen-fixing algae (Dillon et al. 1978; Michalski and Conroy 1973). Further support for these findings were those of Jones (1979) who discovered that the growth of *A. flos-aquae* in eutrophic waters was related to the duration of the depletion of nitrate-nitrogen in the water. Also, Schindler (1977) showed that fertilization of a lake with the low nitrogen to phosphorus ratio fertilizer promoted the growth of the nitrogen-fixer *A. flos-aquae*.

In the Bay of Quinte, a further substantial increase in ambient inorganic nitrogen may be necessary to diminish noticeably the competitive advantage which the nitrogen-fixing algae now apparently have. Further reductions in phosphorus loading will be necessary to achieve this, but an additional increase in inorganic nitrogen will undoubtedly also be encouraged by a continued increase in atmospheric deposition of NO_x which has likely contributed to major increases in $NO_3 - N$ in Lake Ontario (Dobson 1981) in the past two decades.

The decrease since 1977 in bloom forming blue-green algae and associated enhancement of aesthetic quality in the Bay of Quinte is undoubtedly associated with improved quality of the "raw" water at the Belleville water treatment plan. Odour problems, in the past associated mainly with high densities of *Aphanizomenon* and *Anabaena*, have been less severe since 1977. Other major benefits related more generally to plant operation include much less dependence on microstrainers for removal of algae ahead of the sand filtration beds. Microstrainers (four units totalling $3 \times 10^4 m^3/d$) were used for a 4-to-5-mo period during the summers of the 1960's and 1970's; but, since 1977, the microstrainers have been needed for only 4–6 wk each year when densities of *Melosira*, *Anabaena*, and *Aphanizomenon* caused clogging of sand filter beds.

As a result of the phosphorus reduction program, the potential cost savings to municipalities dependent on the Bay of Quinte for potable water are probably substantial. Discussions had taken place in the late 1960's and early 1970's concerning a drinking water pipeline from Lake Ontario to Belleville (Ontario Ministry of the Environment and Belleville Utilities Commission, data and correspondence files). Clearly, had the phytoplankton densities not declined after 1977, the pipeline or other similarly costly proposals would have been given more serious consideration.

The other major consequences of the blue-green algal reductions in the Bay of Quinte relate to the "food chain" and the suitability of the phytoplankton community as a food source for higher trophic levels. Although some secondary producers, such as anuran larvae, are apparently able to ingest blue-green algae as readily as other algae (Seale and Beckvar 1980), Arnold (1971), Porter (1977), and others have shown that colonial blue-greens such as *Anabaena* spp. are poorly utilized or rejected by suspension feeders such as microcrustacean zooplankton organisms which are generally considered the next major "link" (above algae) in aquatic systems. It is conceivable that high densities of filamentous forms could interfere with the normal filtration mechanisms of cladocerans and lead to suboptimal levels of food intake by these organisms even in the presence of adequate supplies of suitable food items. Chrysomonads and cryptomonads, which are mainly small, unicellular species lacking rigid cellulose walls, but storing lipids, oils (e.g. laminarin), and/or starches, are probably used to best nutritional advantage by filter-feeding zooplankton in the Bay of Quinte and other waters. No doubt other taxa are utilized as well (e.g. coccoid greens) but probably less efficiently.

The blue-green bloomers, on the other hand, likely represent the algal group with the lowest food chain utility. These algae are (mainly) large colonial forms, many of which are toxin producers, thus adding to their undesirability in aquatic systems (Carmichael 1981). Again, there are unquestionably other taxa which are poorly utilized, such as large diatoms and dinoflagellates, but in the interest of developing a simple index (*F* index) which can be used to indicate the desirability of the phytoplankton composition in energy flow and food chain function, only the three groups (Chrysophyceae, Cryptophyceae, and blue-green bloomers) were used.

Relative increases in the Chrysophyceae after 1977 in the Bay of Quinte suggest that species of this group are better able to compete for nutrients under phosphorus-limiting conditions. Increases in Chrysophyceae were also observed in Gravenurst Bay following phosophorus loading controls (Dillon et al. 1978), and De Noyelles and O'Brien (1978) found that fertilization of ponds led to decreases in Chrysophyceae but increases in green and blue-green algae. The increases in the *F* index in the Bay of Quinte indicate a shift in community structure to one which is more food chain functional.

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References

APHA. 1960. Standard methods for the examination of water and wastewater. 13th ed. American Public Health Association, Washington, DC.

Arnold, D. E. 1971. Ingestion, assimilation, survival and reproduction by *Daphnia pulex* fed seven species of blue-green algae. Limnol. Oceanogr. 16: 906–920.

Bailey-Watts, A. E. 1976. Planktonic diatoms and silica in Loch Leven, Kinross, Scotland: a one month silica budget. Freshwater Biol. 6: 203–213.

Barica, J. 1975. Collapses of algal blooms in prairie pothole lakes: their mechanism and ecological impact. Verh. Int. Ver. Limnol. 19: 606–615.

Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72: 156–181.

Bray, J. R., and J. T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349.

Canfield, D. E., and R. W. Bachmann. 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. Can. J. Fish. Aquat. Sci. 38: 414–423.

Carmichael, W. W. 1981. Freshwater blue-green algae, p. 1–13. *In* W. W. Carmichael [ed.] The water environment; algal toxins and health. Plenum Press, New York, NY.

Christie, A. E. 1973a. Phytoplankton studies in the Bay of Quinte: I — physical, chemical and phytoplankton characteristics. Res. Rep. W44, Ministry of the Environment, Toronto, Ont. 55 p.

1973b. Phytoplankton studies in the Bay of Quinte: II — relationships between seston–phosphorus, nitrogen, carbon and phytoplankton. Res. Rep. W45, Ministry of the Environment, Toronto, Ont. 30 p.

Cook, D. G., and M. R. McComas. 1974. Geologic, hydrological and limnological description of the Twin Lakes Watershed. North American Project Report, U.S. EPA, Corvallis, OR.

Coveney, M. F., G. Cronberg, M. Enell, K. Larsson, and L. Olofsson. 1977. Phytoplankton, zooplankton and bacteria — standing crop and production relationships in a eutrophic lake. Oikos 29: 5–21.

Cronberg, G. 1982. Changes in the phytoplankton of Lake Trummen induced by restoration. Hydrobiologia 86: 185–193.

De Groot, W. T. 1981. Phosphate and wind in a shallow lake. Arch. Hydrobiol. 91: 475–489.

De Noyelles, F., and W. F. O'Brien. 1978. Phytoplankton succession in nutrient enriched experimental ponds as related to changing carbon, nitrogen and phosphorus conditions. Arch. Hydrobiol. 81: 137–165.

Dillon, P. J., K. H. Nicholls, and G. W. Robinson. 1978. Phosphorus removal at Gravenhurst Bay, Ontario: an 8-year study on water quality changes. Verh. Int. Ver. Limnol. 20: 263–271.

Dobson, H. 1981. Trophic conditions and trends in the Laurentian Great Lakes. W.H.O. Water Qual. Bull. 6: 146–151, 158, 160.

Edmondson, W. T. 1979. Lake Washington and the predictability of limnological events. Arch. Hydrobiol. Beih. 13: 234–241.

Haffner, G. D. 1977. The production ecology of *Stephanodiscus astraea* (Ehrenb.) Grun. Hydrobiologia 54: 247–255.

Hakansson, H., and S. Locker. 1981. *Stephanodiscus* Ehrenberg 1846, a revision of the species described by Ehrenberg. Nova Hedwigia 35: 117–150.

Horne, A. J. 1979. Management of lakes containing N_2-fixing blue-green algae. Arch. Hydrobiol. Beih. 13: 133–144.

Hurley, D. A., and W. J. Christie. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Janus, L. L., and R. A. Vollenweider. 1981. The OECD Cooperative Programme on Eutrophication, Canadian Contribution. Sci. Ser. No. 131, National Water Research Institute, Canada Centre for Inland Waters, Burlington, Ont.

Johnson, M. G., and D. A. Hurley. 1986. Overview of Project Quinte — 1972–82, p. 1–6. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G. and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

Jones, R. I. 1979. Notes of the growth and sporulation of a natural population of *Aphanizomeron flos-aquae*. Hydrobiologia 62: 55–58.

Kalff, J. and R. Knoechel. 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. Annu. Rev. Ecol. Syst. 9: 475–495.

Kilham, P. 1971. A hypothesis concerning silica and the freshwater planktonic diatoms. Limnol. Oceanogr. 16: 10–18.

Kilham, P., and D. Tilman. 1979. The importance of resource competition and nutrient gradients for phytoplankton ecology. Arch. Hydrobiol. Beih. 13: 110–119.

Klaveness, D., and R. R. L. Guillard. 1975. The requirement for silicon in *Synura petersenii* (Chrysophyceae). J. Phycol. 11: 349–355.

LaZerte, B. D. 1980. The stationary phase of a natural population of *Asterionelle formosa* (Bacillariophyceae) limited by silica. Arch. Hydrobiol. 90: 26–38.

Lean, D. R. S., C.F-H. Liao, T. P. Murphy, and D. S. Painter. 1978. The importance of nitrogen fixation in lakes. Ecol. Bull. (Stockholm) 26: 41–51.

Lund, J. W. G. 1971. An artificial alteration of the seasonal cycle of a plankton diatom *Melosira italica* subsp. *subarctica* in an English lake. J. Ecol. 59: 521–533.

Lund, J. W. G., C. Kipling, and E. D. LeCren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiol 11: 143–170.

Lund, J. W. G., C. Kipling, and E. D. LeCren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143–170.

McCombie, A. M. 1967. A recent study of the phytoplankton of the Bay of Quinte 1963–1964. Proc. 10th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. 1967: 37–62.

Michalski, M. F. P., and N. Conroy. 1973. The "oligotrophication" of Little Otter Lake, Parry Sound District. Proc. 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. 1973: 934–948.

Millard, E. S. 1986. Seasonal trends in turnover times of orthophosphate in the Bay of Quinte, Lake Ontario, p. 91–99. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario, Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario, Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Munawar, M., and I. F. Munawar. 1981. A general comparison of the taxonomic composition and size analyses of the phytoplankton of the North American Great Lakes. Verh. Int. Ver. Limnol. 21: 1695–1716.

Nicholls, K. H. 1976a. Nutrient–phytoplankton relationships in the Holland Marsh, Ontario. Ecol. Monogr. 46: 179–199.

1976b. The phytoplankton of the Kawartha Lakes (1972 and 1976), p. 29–45. *In* Kawartha Lakes Water Management Study. Chap. 2. Ontario Ministry of the Environment/Ontario Ministry of Natural Resources, Toronto, Ont. 185 p.

1985. A measure of plankton community similarity utilizing variable weighting of total density and taxonomic proportionality. Int. Rev. Gesamten Hydrobiol. 5: 621–632.

Nicholls, K. H., and E. C. Carney. 1979. The taxonomy of Bay of Quinte phytoplankton and the relative importance of common and rare taxa. Can. J. Bot. 57: 1591–1608.

1986. Nitrogen and phosphorus limitation to phytoplankton in the Bay of Quinte and implications for phosphorus loading controls, p. 139–144. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario, Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H. and P. J. Dillon. 1978. An evaluation of phosphorus–chlorophyll–phytoplankton relationships for lakes. Int. Rev. Gesamten Hydrobiol. 63: 171–154.

Nicholls, K. H., and L. Heintsch. 1986. A comparison of the net phytoplankton in the lower Bay of Quinte near Indian Point, 1945 and 1981, p. 159–165. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario, Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H., D. W. Standen, and G. J. Hopkins. 1980. Recent changes in the near-shore phytoplankton of Lake Erie's western basin at Kingsville, Ontario. J. Great Lakes. Res., Int. Assoc. Great Lakes Res. 6: 146–153.

Oglesby, R. T. 1977. Phytoplankton summer standing crop and annual productivity as functions of phosphorus loading and various physical factors. J. Fish. Res. Board Can. 34: 2255–2270.

Olrik, K. 1973. Phytoplankton from four culturally influenced lakes of the Møllea Lake system, North Zealand, Denmark. Bot. Tidsskr. 68: 1–29.

Olsén, P., and E. Willén. 1980. Phytoplankton response to sewage reduction in Vättern, a large oligotraphic lake in central Sweden. Arch. Hydrobiol. 89: 171–188.

Porter, K. G. 1977. The plant–animal interface in freshwater ecosystems. Am. Sci. 65: 159–170.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario, Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Schindler, D. W. 1977. Evalution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnol. Oceanogr. 23: 478–486.

Schindler, D. W. and G. W. Comita. 1972. The dependence of primary production upon physical and chemical factors in a small senescing lake, including the effects of complete winter oxygen depletion. Arch. Hydrobiol. 69: 413–451.

Schindler, D. W. and E. J. Fee. 1974. Experimental lakes area: whole-lake experiments in eutrophication. J. Fish. Res. Board Can. 31: 937–953.

Schindler, D. W., H. Kling, R. V. Schmidt, J. Prokopowich, V. E. Frost, R. A. Reid, and M. Capel. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth year of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

Seale, D. B., and N. Beckvar. 1980. The comparative ability of anuran larvae (Genera: *Hyla*, *Bufo* and *Rana*) to ingest suspended blue-green algae. Copeia 1980(3): 495–503

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science (Wash., DC) 221: 669–671.

Sorensen, T. 1948. A method for establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. K. Dansk. Vidensk. Selsk. Biol. Skrift. 5: 3–16.

Swale, E. M. F. 1963. Notes on *Stephanodiscus hantzschii* Grun. in culture. Arch. Mikrobiol. 45: 210–216.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58: 338–348.

1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62: 802–815.

Tucker, A. 1948. The phytoplankton of the Bay of Quinte. Trans. Am. Microsc. Soc. 67: 365–383.

Vollenweider, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD (Paris) Tech. Rep. DAS/CSI/68.27.

WHITTAKER, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 42: 207–264.

WILLÉN, E. 1976. A simplified method of phytoplankton counting. Br. Phycol. J. 11: 265–278.

WRIGHT, D. G. 1976. Wind induced regeneration of phosphorus from the sediments of the upper Bay of Quinte. M.Sc. thesis, University of Guelph, Guelph, Ont. 62 p.

A Comparison of the Net Phytoplankton in the Lower Bay of Quinte Near Indian Point, 1945 and 1981

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Birge and Juday plankton trap collections of net phytoplankton from the lower Bay of Quinte were made in 1981 in order to duplicate collections and analyses made by A. Tucker at the same site in 1945. By 1945, a significant eutrophication of the Bay of Quinte had taken place but had not yet reached the worse-case conditions of the 1950's and 1960's. Differences in average densities of total phytoplankton, diatoms, green algae, and blue-green algae during the June–October periods of 1945 and 1981 were not statistically significant (*t*-tests, $P \leq 0.05$). The genera recorded by Tucker in 1945 were again the dominant components of the phytoplankton in 1981. The inclusion of 35 additional genera and several small unidentified chrysomonads found in 1981, but either not present or not detected in 1945, did not alter significantly the total phytoplankton density of 1981 relative to the 1945 average density. The June–October average density of the diatom *Fragilaria* was significantly greater in 1981 than in 1945, while the early summer (June and July) average density of *Melosira* was significantly greater in 1945. Blue-green algae, predominantly *Aphanizomenon* and lesser densities of *Anabaena* and *Lyngbya*, were significantly more abundant during the early summer of 1981 than during 1945, suggesting a more eutrophic status in 1981 than in 1945. However, recent data from the same region (1973–1977) suggest that similar changes have occurred independently of major changes in phosphorus loading and may, therefore, be within the range of "normal" year-to-year variability.

En 1981, Birge et Juday ont effectué des collectes de microphytoplancton dans la partie inférieure de la baie de Quinte, à l'aide d'un filet à plancton, en vue de répéter les collectes et les analyses faites par A. Tucker au même endroit en 1945. Vers 1945, il y avait eutrophisation prononcée de la baie de Quinte, mais elle n'avait pas encore atteint les niveaux observés pendant les années 50 et 60. Les différences enregistrées dans les densités moyennes du phytoplancton total, des diatomées, des algues vertes et des algues bleues entre les mois de juin et octobre en 1945 et en 1981 n'étaient pas significatives du point de vue statistique (tests de *t*, $P \leq 0{,}05$). Les éléments dominants du phytoplancton en 1981 comprenaient les mêmes genres que ceux qui avaient été signalés par Tucker en 1945. Le fait d'inclure 35 genres additionnels et plusieurs petites chrysophycées non identifiées découvertes en 1981, qui n'étaient pas présentes ou n'avaient pas été décelées en 1945, n'a pas modifié de façon sensible la densité du phytoplancton total en 1981 par rapport à la densité moyenne enregistrée en 1945. La densité moyenne de la diatomée *Fragilaria* entre juin et octobre était beaucoup plus grande en 1981 qu'en 1945, alors que la densité moyenne de *Melosira* au début de l'été (juin et juillet) était beaucoup plus grande en 1945. Les algues bleues, principalement *Aphanizomenon*, de même que *Anabaena* et *Lyngbya* en densités plus faibles, étaient beaucoup plus abondantes au début de l'été 1981 qu'en 1945, ce qui porte à croire que l'eutrophisation était plus prononcée en 1981 qu'en 1945. Cependant, des données récentes provenant de la même région (de 1973 à 1977) laissent supposer que des changements semblables ont eu lieu indépendamment des changements importants dans les apports de phosphore et qu'ils pourraient par conséquent se situer dans l'échelle des variations « normales » observées d'une année à l'autre.

Introduction

Aside from evidence obtained through paleolimnological investigations (e.g. Harris and Vollenweider 1982; Stoermer et al. 1985), there are few long-term data available for the assessment of changes in phytoplankton and trophic status of the Great Lakes (Nicholls 1981). In the summer of 1945, Allan Tucker collected phytoplankton at the lower end of Adolphus Reach in the Bay of Quinte near Indian Point (Tucker 1948). The results of these early analyses were felt to be relevant to modern day phytoplankton densities and composition at this site, since considerable changes in human population and associated nutrient loading to the Bay of Quinte have taken place in the intervening 35 yr (Johnson and Owen 1971); Minns 1986). More recently, a significant reduction in phosphorus loading from municipal sewage treatment plants has been achieved (Minns et al. 1986), and corresponding changes in the phytoplankton of the Bay of Quinte have resulted (Nicholls et al. 1986).

This study of the phytoplankton of the lower Bay of Quinte was undertaken in 1981 so that the modern day net phytoplankton community could be compared with results from an identical study completed prior to the development of major trophic status and fisheries problems. Most of the discussion of total phytoplankton – trophic state relationships (including nannoplankton) in the Bay of Quinte is presented in Nicholls et al. (1986). The objective of this paper is to compare the abundance of large (net) phytoplankton species (1945 vs. 1981), identifiable and quantifiable by Tucker's (1947, 1948) methods.

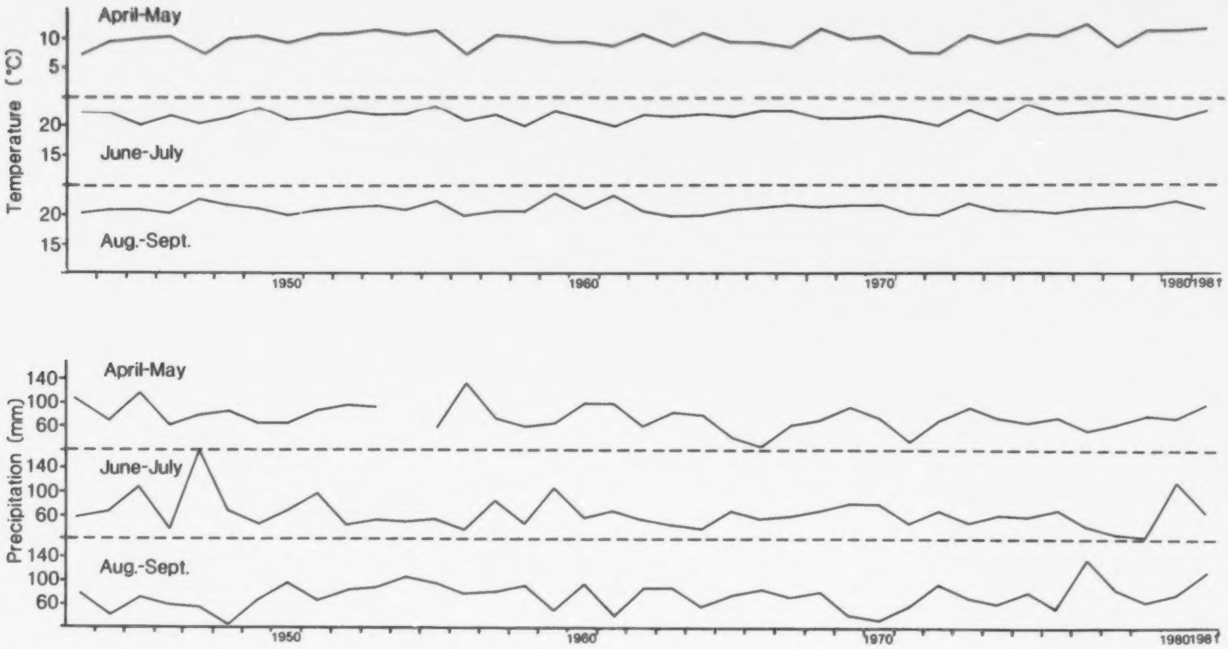

FIG. 1. Upper: bimonthly average water temperatures in the upper Bay of Quinte for the April–September periods of 1943 to 1981 sampled through the Belleville municipal water intake. Lower: bimonthly total precipitation at Belleville over the same period.

Methods

Sampling and analysis procedures followed those outlined by Tucker (1948). At weekly intervals from June to October, Tucker's 1945 station (44°07′10″ N, 71°52′10″ W) was sampled at 0, 10, 20, 30, and 40 m depth using a 10-L Birge and Juday plankton trap fitted with number 20 bolting cloth. We fixed phytoplankton samples immediately after collection with Lugol's solution. Tucker apparently did not use Lugol's solution. However, differences in results attributable to different fixatives and preservatives are only important as they relate to long-term storage of samples and the preservation of some small flagellates and other delicate forms; neither condition was important in this study of net phytoplankton.

Analyses followed Tucker's unit system (his table 5) except that an inverted microscope with magnifications of 300 and 600 × was used for enumeration. Those taxa found in 1981 but apparently not considered by Tucker were assigned unit values based on morphology relative to those taxa listed by Tucker (his table 5; single cells and single colonies = 1 unit, 100 or 300 μm length of filamentous forms (depending on the genus) = 1 unit). In assigning unit values to genera recorded in 1981 but not in 1945, some reluctance to follow Tucker's guidelines entirely (i.e. single cell = 1 unit) for small forms not recorded by him led to our separate tabulation of some species (mainly chrysomonads) and their exclusion from the total for purposes of direct comparison of the two data sets. These additional taxa were treated separately in statistical comparisons of 1981 and 1945 results, since it was found that the detection of many of the additional smaller sized taxa in 1981 samples was a direct result of using the higher magnification of the inverted microscope.

For comparative purposes (1945 vs. 1981), 1981 counts of ***Stephanodiscus binderanus*** (Kutz.) Krieger were included in ***Melosira***, since its removal from ***Melosira*** (as ***M. binderana*** Kutz.) has been recognized only relatively recently (Round 1972). Other taxonomic considerations were as reported in Nicholls and Carney (1979).

Since Tucker (1948) reported very few data (as numbers), we also referred to his thesis tables 7–42 (Tucker 1947) for statistical comparisons with 1981 data. These comparisons were made with *t*-tests, the use of which was justified by the approximately normal though very broad distribution of some data.

Water temperatures (Hydrolab) and Secchi disc visibilities recorded in 1981 at nearby Project Quinte Station C were not duplicated at Tucker's station in 1981, since data collected during June–August of 1980 showed no significant differences between these two adjacent sites.

Results

Climate, Water Temperature, and Secchi Disc Visibility

Long-term records of precipitation at Belleville and of Bay of Quinte water temperatures recorded at the Belleville municipal water intake show considerable year-to-year variability over the 1943–81 period (Fig. 1). For example, the midsummer periods of 1947 and 1980 were unusually wet, while 1946 and 1979 were unusually dry. Extremes of precipitation and temperature were not evident for either 1945 or 1981, and comparisons of phytoplankton composition and densities can probably be made independently of weather effects for these two years.

From the data available, a detailed comparison of water temperatures in the lower Bay of Quinte in 1945 and 1981 is difficult, owing to irregularity of data collection and the apparent influence of incursions of Lake Ontario water into the Bay of Quinte (Freeman and Prinsenberg 1986). However, no major differences between the two years in vertical thermal regimes are apparent (Fig. 2). The surface waters may have warmed sooner in 1981 than in 1945, with temperatures of the upper 20 m ranging between 8 and 13°C on 3 June 1981, but only

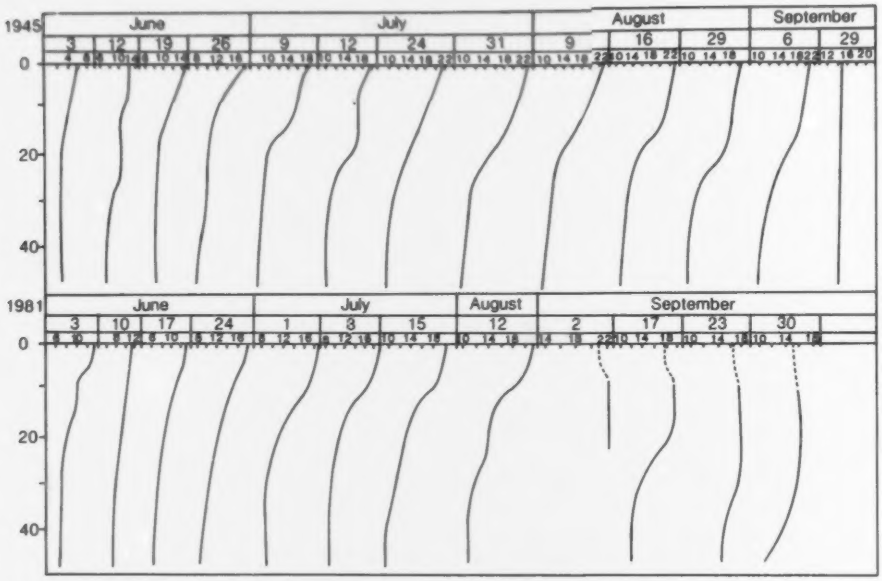

FIG. 2. Vertical water temperature profiles (smoothed from original data) at the Indian Point sampling station in the outer Bay of Quinte during 1945 and at adjacent Project Quinte Station C during 1981.

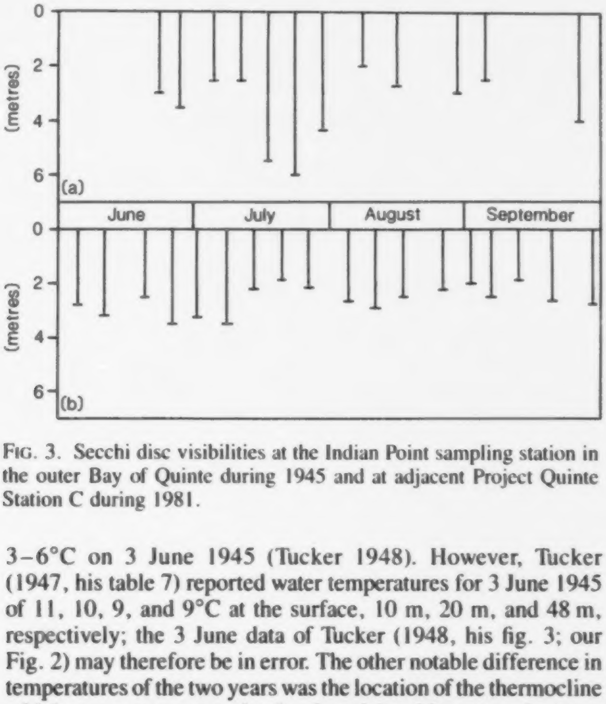

FIG. 3. Secchi disc visibilities at the Indian Point sampling station in the outer Bay of Quinte during 1945 and at adjacent Project Quinte Station C during 1981.

3–6°C on 3 June 1945 (Tucker 1948). However, Tucker (1947, his table 7) reported water temperatures for 3 June 1945 of 11, 10, 9, and 9°C at the surface, 10 m, 20 m, and 48 m, respectively; the 3 June data of Tucker (1948, his fig. 3; our Fig. 2) may therefore be in error. The other notable difference in temperatures of the two years was the location of the thermocline which was never strongly developed in either year, but was positioned about 5 m higher in the water column in 1981 than in 1945 (Fig. 2), undoubtedly as a result of the faster rate of warming of the surface waters in 1981. By the end of September of 1945, the water column was homothermous at about 14°C, but had not yet completely mixed by this date during 1981 (Fig. 2).

Secchi disc visibilities (Fig. 3) during 1945, averaging 3.5 ± 1.3 m, were significantly better than those recorded for the June–October period of 1981 (2.6 ± 0.5 m), owing mainly to three high values during the last 2 wk of July 1945 (t-test, $P \leq 0.05$).

Phytoplankton

There were no significant differences between the 1945 and 1981 June–October average densities of total phytoplankton, green algae, blue-green algae, and diatoms (Table 1). Total phytoplankton maxima occurring in July of 1945 and September of 1981 were nearly identical. Of the three dominant classes, diatoms were the most important component of the total during both years (73 and 60%), followed by blue-green algae (16 and 24%) and green algae (9 and 6%).

Many of the characteristics of the 1981 diatom community appear to be little changed from 1945. The three dominant genera in 1945, *Melosira*, *Tabellaria*, and *Fragilaria*, were again the most important during 1981 although their relative densities were altered somewhat (Table 1). In particular, the 1981 *Fragilaria* average density of 2138 units · L^{-1} was significantly greater than the 1151 units · L^{-1} recorded for 1945. The seasonality of *Melosira* was quite different between the two years (Fig. 4); the early summer (June and July) average density was significantly greater during 1945 than during 1981 (Table 1). In contrast, the seasonality of *Tabellaria* (Fig. 4) and *Asterionella* appears to have changed little; both were early summer forms. The *Asterionella* maximum of 2435 units · L^{-1} occurred on 3 June 1981 and declined thereafter so that densities of less than 166 units · L^{-1} were present after the third week of June. Similarly, the *Tabellaria* maxima (Table 1) occurred in June of both 1945 and 1981 and were followed by much lower densities, none of which in 1981 exceeded 530 units · L^{-1} after mid-July.

Diatoma (Tucker's *Odontidium*) showed highest densities in early June of 1981 (952, 475, and 300 units · L^{-1} on the first three sampling dates, but then declined and, except for two September values of 287 and 321 units · L^{-1}, was generally less than 50 units · L^{-1} for the rest of the sampling period.

Other diatom genera including *Navicula*, *Stephanodiscus*, and *Synedra*, which were minor components of the flora in

TABLE 1. Maximum and mean ± 1 SD phytoplankton densities (units · L^{-1} during the June through September periods of 1945 and 1981 (except where indicated). Data are from averages of five sampling depths near Indian Point. Only where indicated are differences significant.

	1945		1981	
	Maximum	Mean ± 1 SD	Maximum	Mean ± 1 SD
Total phytoplankton[a]	20 798	10 874 ± 5 619	24 285	9 506 ± 4 794
Green algae	6 844	948 ± 2 004	1 727	583 ± 508
Blue-green algae	10 695	1 760 ± 3 340	8 371	2 284 ± 2 122
Diatoms	18 374	7 941 ± 5 469	14 187	5 749 ± 3 834
Melosira	8 766	3 080 ± 2 540	11 268	1 589 ± 3 017
Tabellaria	6 417	2 080 ± 2 208	6 148	1 130 ± 1 637
Fragilaria[b]	4 616	1 151 ± 1 220	5 831	2 494 ± 1 602
Microcystis	2 860	664 ± 1 040	480	101 ± 118
Aphanizomenon	7 309	907 ± 2 238	6 777	1 443 ± 1 626
Blue-green algae[c] (June and July)	154	49 ± 62	2 544	1 427 ± 783
Aphanizomenon[c] (June and July)	<10	<10	1 190	702 ± 372
Melosira[d] (June and July)	8 766	3 836 ± 2 811	970	365 ± 299

[a] Only those taxa considered by Tucker (his table 5) were included in the 1981 totals.

[b] The 1981 average was significantly greater than the 1945 average (*t*-test, $P < 0.05$). None of the other June–September 1981 averages differed significantly from those for 1945.

[c] Significantly greater in 1981 than in 1945 (*t*-test, $P < 0.001$).

[d] Significantly greater in 1945 than in 1981 (*t*-test, $P < 0.01$).

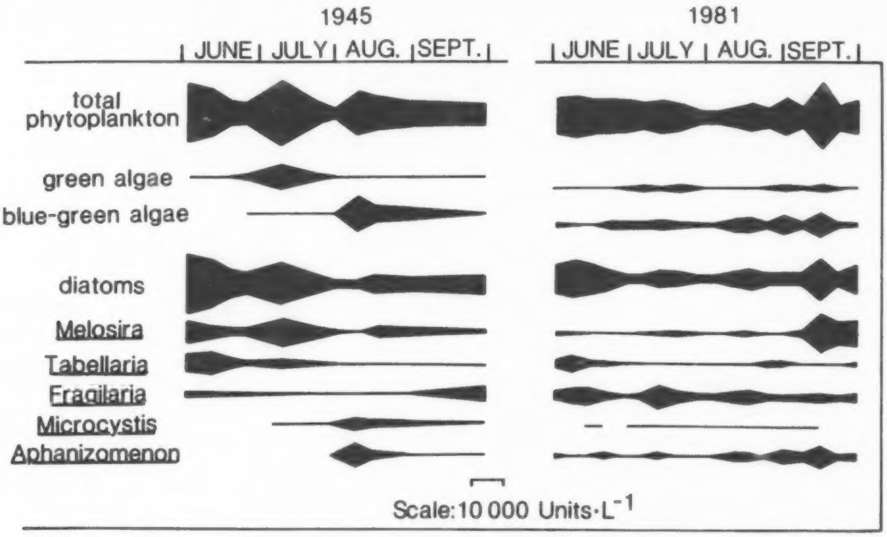

FIG. 4. Densities of dominant phytoplankton taxa at the Indian Point sampling site in the Bay of Quinte, 1945 and 1981. Data include only those genera recorded by Tucker (1948) and are the arithmetic means of the five sampling depths.

1945, were of similar status in 1981. Their combined density on any sampling date during 1981 never exceeded 450 units · L^{-1}.

The dominant blue-green alga at Tucker's sampling station in 1945 and again in 1981 was *Aphanizomenon*. Maximum densities during both years were comparable and mean values did not differ significantly (Table 1). However, the early summer densities during 1981, which ranged between 400 and 1190 units ·L^{-1}, were clearly higher than during the same period of 1945 when the genus was essentially absent (Fig. 4; Table 1). In samples collected in 1963 and 1964, McCombie (1967) also noted an earlier development of blue-green algae than that reported by Tucker (1948).

Anabaena was the second most dominant cyanophyte during 1981, and with an average June–October density of 420 units · L^{-1} appears to have been substantially more abundant than in 1945. Tucker (1948) reported its regular occurrence but "in very small quantities" not exceeding 420 units · L^{-1}. *Anabaena* densities of 1232 and 1576 units · L^{-1} were found on 24 June and 1 July 1981.

Next in order of dominance among the Cyanophyceae in 1981 were *Lyngbya*, *Microcystis*, and *Coelosphaerium*, with average densities of 188 ± 352, 150 ± 276, and 129 ± 236 units · L^{-1}, respectively.

As in 1945, *Mougeotia* was the most important green alga in

TABLE 2. Densities (units · L^{-1}) of other genera (in addition to those listed by Tucker) found in at least five samples during 1981 and with June–October average densities greater than 75 units · L^{-1}. Values listed are from averages of five depths sampled at Tucker's (1948) station.

	Maximum	Mean ± 1 SD
Chlorophycae		
Oedogonium	1 809	276 ± 474
Ulothrix	569	154 ± 157
Chlamydomonas	729	153 ± 209
Cyanophyceae		
Phormidium	558	79 ± 145
Oscillatoria	856	147 ± 216
Bacillariophyceae		
Cyclotella	1 019	95 ± 243
Cryptophyceae		
Cryptomonas	2 988	278 ± 699
Rhodomonas	3 676	373 ± 884

TABLE 3. Maximum and mean ± 1 SD phytoplankton densities (units · L^{-1}) during the June through September period of 1981 (except where indicated). Data are from averages of five sampling depths near Indian Point.

	Maximum	Mean ± 1 SD
Total phytoplankton[a]	26 644	11 423 ± 5 999
Green algae	3 192	1 325 ± 788
Blue-green algae	9 071	2 524 ± 2 326
Diatoms	14 506	5 898 ± 3 936
Blue-green algae[b] (June and July)	2 633	1 535 ± 786

[a] All taxa except small unidentified chrysomonads were included in the total (i.e. the genera recorded for 1945 (Tucker's table 5) as well as 35 additional genera found in 1981).

[b] Significantly different from 1945 (*t*-test, $P < 0.001$).

1981 and, with a June–October average of 393 ± 477 units · L^{-1}, contributed most to the Chlorophyceae. The maxima for this genus (1312 and 1643 units · L^{-1}) occurred on 8 and 23 July. *Pediastrum* and *Scenedesmus* were late summer green algae with combined maxima of less than 450 units · L^{-1} in mid-September.

Among other groups of algae, *Dinobryon* (the only chrysophyte listed by Tucker) was very important during the early summer of 1981, with a maximum of 5380 units · L^{-1} on 1 July when it comprised 54% of the total phytoplankton density. *Dinobryon* achieved densities of between 3650 and 5380 units · L^{-1} for three consecutive weeks, although the June–October average was only 847 units · L^{-1}. In 1945, *Dinobryon* never exceeded 440 units · L^{-1}.

The two genera of dinoflagellates reported by Tucker (1948), *Ceratium* and *Peridinium*, "neither of which exceeded 572 units L^{-1}" in 1945, were also relatively unimportant in 1981, with maximum and average densities of 135 and 17, and 127 and 30 units · L^{-1}, respectively.

Taxa Not Reported by Tucker and Depth Distribution

In addition to the taxa present in Tucker's samples, the 1981 samples contained 35 other genera, as well as some unidentified forms. Fewer than one half of these were quantitatively important (Table 2). The addition of these taxa to those recorded by Tucker results in only relatively small increases in density of the major algal classes found for 1981 (Table 3). These slightly higher densities do not alter any of the levels of significant difference between 1945 and 1981 (Table 1).

For comparative purposes (1945 vs. 1981), another group of algae kept separate from the 1981 totals were the very small chrysomonads (2–5 μm diameter) which cannot be identified at the microscope magnification (160 ×) used by Tucker. With the higher magnifications of the inverted microscope, this group was found to include single cells of *Uroglena*, *Chromulina*, *Ochromonas*, *Kephyrion*, *Chrysochromulina*, and others whose contribution to the total phytoplankton cell volume was clearly insignificant in these net-filtered samples. For example, the two highest densities of small chrysomonads occurred on 24 June and 1 July, with an average density of 8760 cells · L^{-1}. On these two dates, their average contribution to total phytoplankton volume was only 1%.

Although it seemed unreasonable to assign unit values to each small chrysomonad cell as Tucker did for other much larger single cells and colonies of cells in his collections, this was done and yielded an average density of 1286 ± 3569 units · L^{-1} during the June–October period (average of five sampling depths) which still did not alter significantly the 1981 grand mean relative to 1945 (*t*-test).

The highest densities of phytoplankton in 1945 and 1981 were usually found in the upper 10 m; however, on several dates, there was little difference in algal densities between the surface waters and 40 m (Fig. 5 and 6). The vertical distribution was most marked during July and August when very low algal densities at 30–40 m (relative to the 0–10 m values) were accompanied by the greatest range in vertical water temperatures of 8–12°C (Fig. 2).

The temporal change in some vertical profiles suggests a sedimentation loss of certain diatoms during 1981. For example, the mid-July increase in *Fragilaria* from about 1050 units · L^{-1} on 8 July (average of five depths) to its summer maximum of 5830 on 17 July was essentially restricted to the upper 10 m. Its subsequent decline was characterized by a deepening to 20 m of the bulk of the population by 23 July and a further loss, presumably by continued sedimentation, to an average of 1500 units · L^{-1} by 30 July (Fig. 5). Similarly, the seasonal maximum of *Melosira* of 11 270 units · L^{-1} (average of five depths) developed by 17 September at which time it contributed 80% of the diatom density. Subsequent declines in total density were most marked in surface samples on 23 and 30 September, but increased densities were noted at 30 m on the same dates (Fig. 5).

Inclusion of the 35 additional genera found during 1981 with those genera found by Tucker did not alter appreciably the general pattern of vertical distribution found for Tucker's genera alone (compare Fig. 6 and 7).

Discussion

There were apparently only small differences in the densities of dominant phytoplankton species between 1945 and 1981 in the lower Bay of Quinte. The most significant difference between 1945 and 1981 relates to the early summer development of blue-green algae. An important question to be answered is: can this difference be explained by normal year-to-year variability, or does it represent a real long-term change?

Some insight into year-to-year variability can be obtained from examination of data from nearby Station C in the outer Bay of Quinte (Nicholls et al. 1986) over the period 1973–77. By analysis of variance and paired *t*-tests, the June–July average

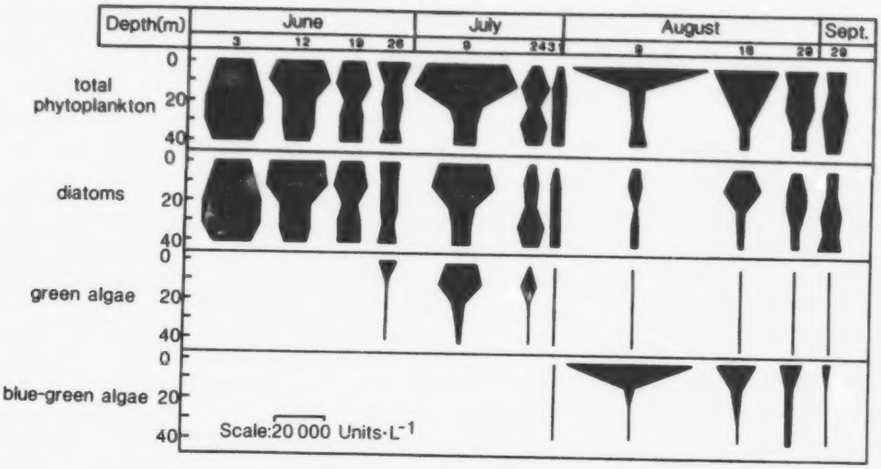

FIG. 5. Vertical distribution of dominant phytoplankton taxa at the Indian Point sampling site in the Bay of Quinte, 1945. Reproduced from Tucker (1948).

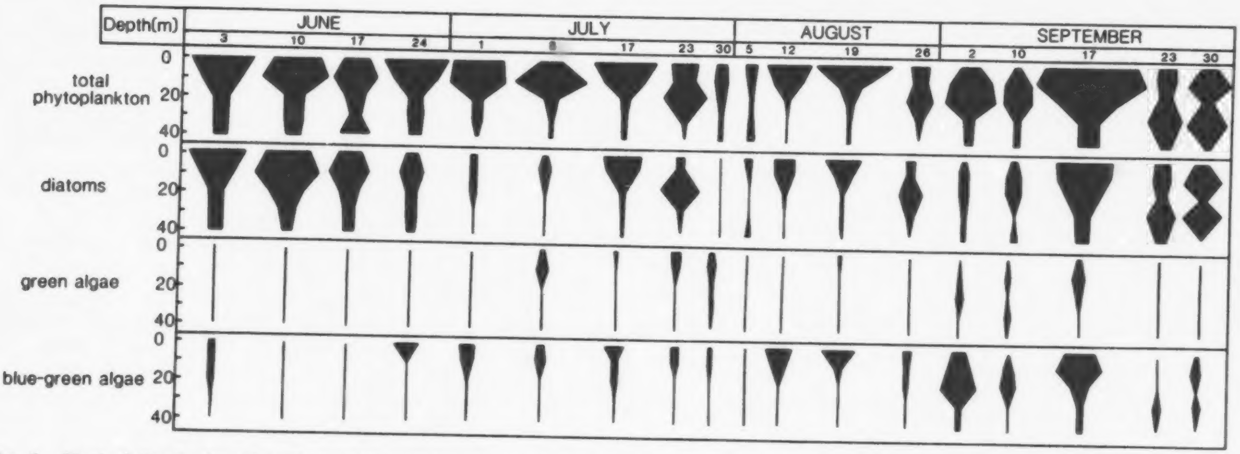

FIG. 6. Vertical distribution of dominant phytoplankton taxa at the Indian Point sampling site in the Bay of Quinte, 1981. Data include only those genera recorded by Tucker (1948). Density scale as in Fig. 5.

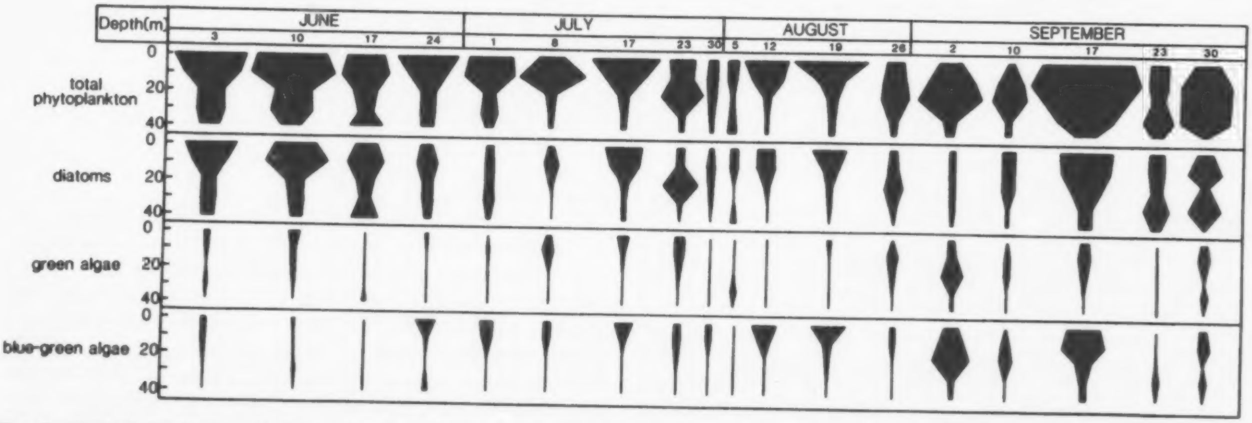

FIG. 7. Vertical distribution of all recorded phytoplankton in the 1981 samples (except for small unidentified chrysomonads) at the Indian Point sampling site in the Bay of Quinte, 1981. Data include the taxa recorded by Tucker (1948) and 35 additional genera. As in Table 3, data on other classes (Chrysophyceae, Dinophyceae, and Cryptophyceae) were included in the total phytoplankton but were not illustrated separately. Density scale as in Fig. 5.

cyanophycean biovolume during 1977 was significantly less ($P < 0.05$) than the June–July average of the other four years. The June–July averages of 1973–76 were not significantly different among themselves. There were no major differences in water temperatures and precipitation during the spring and early summer periods of these years (Fig. 1); neither were there significant changes in phosphorus loading (Minns et al. 1986). It appears that a significant year-to-year difference in early summer biomass of blue-green algae can arise for reasons not related to a change in phosphorus loading. It is possible therefore that the much greater June–July blue-green algal density during 1981 compared with 1945 may not relate to real long-term change in phosphorus loading.

Another important question is: how well does Tucker's Indian Point sampling station represent the lower Bay of Quinte, and is the phytoplankton of this area influenced greatly by independent changes in eastern Lake Ontario?

Those differences that were found between 1945 and 1981 (i.e. significantly higher early summer densities of blue-green algae and of the diatom *Fragilaria* and lower densities of the diatom *Melosira*), while perhaps within the range of expected year-to-year variability, could also indicate changes in Lake Ontario trophic status. Nicholls et al. (1986) noted a progressive decrease in the degree of response of Bay of Quinte phytoplankton to phosphorus loading controls along a five-station gradient from the upper Bay of Quinte to Glenora in the lower bay. However, the response at the sixth station at Conway near the mouth of the Bay of Quinte was as great as at the upper bay stations. This was attributed to a response of Lake Ontario phytoplankton to phosphorus loading controls implemented in Lake Ontario over the same time period.

The nearshore waters of eastern Lake Ontario during spring and early summer are characterized by abundance of *Stephanodiscus binderanus* (= *Melosira binderana*) (Munawar and Munawar 1975; Ontario Ministry of the Environment, unpubl. Kingston intake data). The ratios of all other *Melosira* species to *S. binderanus* at Tucker's station on 3 June and 10 June 1981 were 12:1 and 10:1 (by filament length), respectively. In contrast, the ratios at upper Bay of Quinte Station B were 400–600:1. *Stephanodiscus binderanus* was very rare in the upper Bay of Quinte, and counts of good precision at Station B were not obtained; nevertheless, it is clear that the abundance of *S. binderanus* at Tucker's station is consistent with its known distribution in nearshore Lake Ontario and is in contrast with its scarcity in the upper Bay of Quinte. The phytoplankton at Tucker's station therefore undoubtedly constitutes a blend of eastern Lake Ontario and lower Bay of Quinte assemblages with a dominant influence of Lake Ontario at certain times of the year depending on hydrological and wind influences. Long-term changes that may have occurred in the upper Bay of Quinte phytoplankton over the 1945–81 period are sure to be less easily related to changes at the Indian Point sampling site near Lake Ontario because of the influence of Lake Ontario.

It is important to realize that this 1945 vs. 1981 comparison does not represent a clear "before and after" scenario. The importance of bloom-forming blue-green algae in Tucker's samples suggests that by 1945 the Indian Point region of Lake Ontario–Bay of Quinte was already greatly influenced by eutrophication. In fact, the first recorded evidence of blue-green blooms in the Bay of Quinte predate Tucker's study by four decades (Nicholls et al. 1986). It should be emphasized, therefore, that the 1945 data provide us with an opportunity to compare present data with an earlier period after significant effects of eutrophication had already taken place. These 1945 conditions likely preceded worse conditions which developed after significant human population growth and more widespread use of phosphate detergents in the Bay of Quinte basin during the 1950's and 1960's.

Similarly, 1981 does not represent the Bay of Quinte at its worst. By 1981 the combined effects of phosphorus loading controls in Lake Ontario and in the Bay of Quinte had achieved significant reduction in total phytoplankton biomass in the outer Bay of Quinte (Nicholls et al. 1986) such that the densities of the most abundant net phytoplankton algae were very similar to those found in 1945.

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References

Freeman, N. G., and S. J. Prinsenberg. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Harris, G. P., and R. A. Vollenweider. 1982. Paleolimnological evidence of early eutrophication of Lake Erie. Can. J. Fish. Aquat. Sci. 39: 618–626.

Johnson, M. G., and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

McCombie, A. M. 1967. A recent study of the phytoplankton of the Bay of Quinte. Proc. 10th Conf. Great Lakes Research, Int. Assoc. Great Lakes Res. 1967: 37–62.

Minns, C. K. 1986. Total phosphorus loading to the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Munawar, M., and I. F. Munawar. 1975. Some observations on the growth of diatoms in Lake Ontario with emphasis on *Melosira binderana* Kutz. during thermal bar conditions. Arch. Hydrobiol. 75: 490–499.

Nicholls, K. H. 1981. Recent changes in the phytoplankton of Lakes Erie and Ontario. Proc. Conf. on Changes in the Biota of Lakes Erie and Ontario. Bull. Buff. Soc. Nat. Sci. 25: 41–88.

Nicholls, K. H., and E. C. Carney. 1979. The taxonomy of Bay of Quinte phytoplankton and the relative importance of common and rare taxa. Can. J. Bot. 57: 1591–1608.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Round, F. E. 1972. *Stephanodiscus binderanus* (Kutz.) Krieger, or *Melosira binderana* Kutz. (Bacillarophyta, Centrales). Phycologia 11: 109–117.

Stoermer, E. F., J. A. Wolin, C. L. Schelske, and D. J. Conley. 1985. Postsettlement diatom succession in the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. 42: 754–767.

Tucker, A. 1947. The phytoplankton of the Bay of Quinte. M.A. thesis, part I, Department of Zoology, University of Toronto, Toronto, Ont. 80 p.

1948. The phytoplankton of the Bay of Quinte. Trans. Am. Microsc. Soc. 67: 365–383.

Population Dynamics, Biomass, and Production of the Macrozooplankton in the Bay of Quinte During Changes in Phosphorus Loadings

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The Bay of Quinte on Lake Ontario has become "culturally eutrophic" in the last 100 yr because of excess input of phosphorus. The macrozooplankton community is dominated by small-bodied cladocerans such as *Eubosmina coregoni, Bosmina longirostris*, and *Chydorus sphaericus* in both the shallow hypereutrophic upper part of the bay and in the deeper mesotrophic lower part of the bay. It was anticipated that species composition and production by zooplankton would change in response to scheduled reduction in phosphorus removal which began in 1978. As of the 1983 field season, no such major changes have been recorded. It may be that predation of zooplankton plays a greater role than trophy in determining overall production and species composition at this point of the bay's recovery.

La baie de Quinte du lac Ontario a été eutrophisée au cours des 100 dernières années par des rejets anthrogènes excessifs de phosphore. La communauté macrozooplanctonique est dominée par de petits cladocères tels *Eubosmina coregoni, Bosmina longirostris* et *Chydorus sphaericus*, ceci tant dans sa partie supérieure hyper-eutrophe peu profonde que dans sa partie inférieure mésotrophe plus profonde. On avait prévu une modification de la composition des espèces et de la production du zooplancton en fonction du calendrier des mesures de réduction des rejets de phosphore appliquées en 1978. Aucune variation appréciable n'a cependant pu être notée au cours de la saison de travaux sur le terrain de 1983. Il est possible que la prédation du zooplancton soit plus déterminante, au niveau de la production globale et de la composition en espèces, que ne l'est l'enrichissement, à cette étape-ci du rétablissement de la baie.

Introduction

"Project Quinte" (Johnson and Hurley 1986) is a multiyear study of the response of the Bay of Quinte ecosystem, badly degraded by cultural eutrophication, to a phosphorus reduction program. This study presented us with an opportunity to quantify responses by the zooplankton to anticipated changes in the Bay of Quinte's trophic status. The purpose of this paper is to describe the species composition and production of the macrozooplankton community before and after the implementation of tertiary phosphorus control in 1978.

Preliminary sampling on this community had been carried out in the mid-1960s and again early in the 1970s. These data, most of which have never been published, indicated that the Bay of Quinte was totally dominated by small-bodied cladocerans in the shallow upper or hypereutrophic part of the system. Our own sampling, which began in 1975, before any control of phosphorus was implemented (Minns et al. 1986), confirmed these findings.

We postulated that phosphorus control would have an impact on the phytoplankton and fish communities and this would in turn lead to quantifiable changes in the zooplankton. Assuming the bay became measurably less eutrophic, we anticipated that changes were likely to occur in one or more of the following ways: a change in overall species composition with a shift away from the total domination of the system by small cladocerans such as *Eubosmina*, *Bosmina*, and *Chydorus* and a drop in overall secondary production. We anticipated that whatever changes did occur would be restricted to the upper part of the system because the water quality in the lower bay was not expected to change as a result of the planned phosphorus control. A decision was taken early in the program to monitor stations in the upper and lower bay and also at an intermediate station between the two extremes.

The Bay of Quinte ecosystem has been described in detail in other papers in this volume (Robinson 1986; Hurley 1986; Nicholls et al. 1986). Briefly summarized, the upper bay (as represented by sampling stations Belleville and Napanee (Fig. 1)) is shallow with a maximum depth of approximately 5 m, and in the years prior to the implementation of tertiary phosphorus treatment in 1978 (i.e. pretreatment years of 1975 and 1976 for this study) was hypereutrophic. In the post-treatment years from 1979 to the present the water quality could best be described as eutrophic. The midpart of the Bay of Quinte ecosystem, as represented by our Hay Bay station, has a maximum depth of approximately 11.5 m and in both pre- and post-treatment years could be characterized as eutrophic although there were measurable improvements in water quality following phosphorus control. The lower bay stations of Glenora and Conway have maximum depth of 21 and 32 m, respectively. The water quality of these two stations was only slightly changed in the post-treatment years at Glenora and not at all at Conway.

Materials and Methods

All zooplankton samples were collected during the weekly

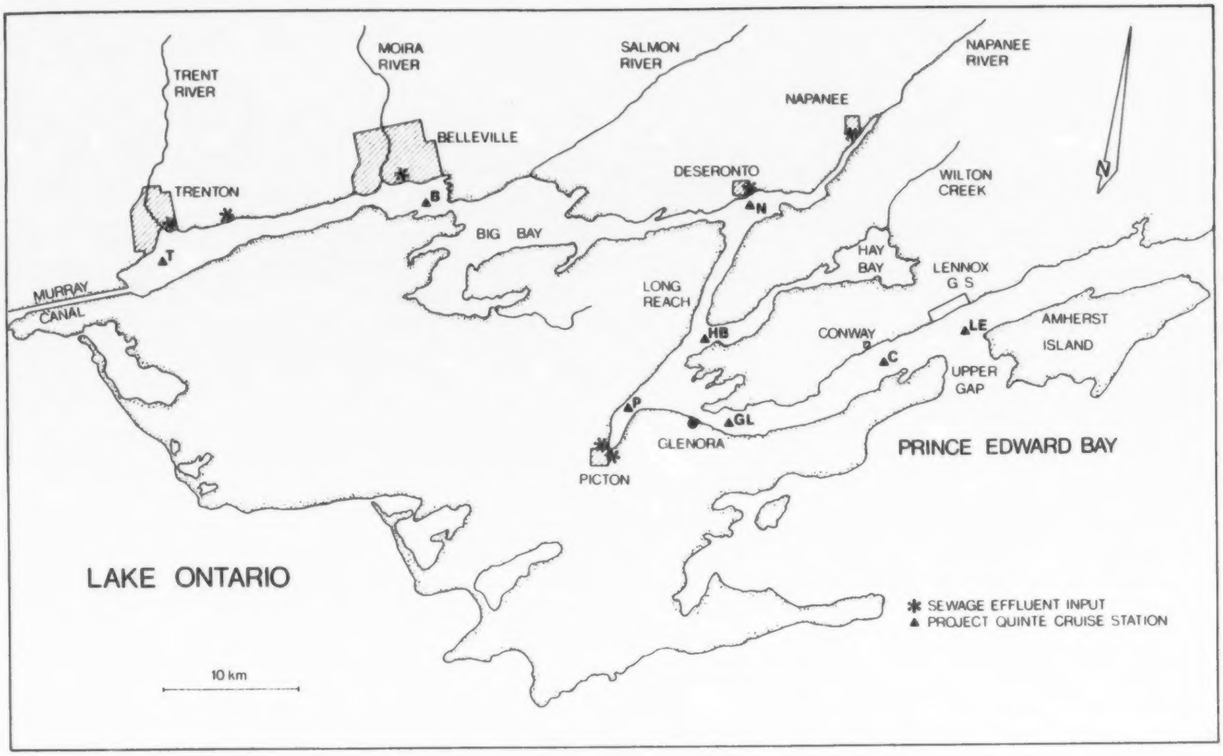

FIG. 1. Bay of Quinte showing the "Project Quinte" cruise stations where zooplankton were collected.

Project Quinte sampling cruises from May to September as described by Millard and Johnson (1986). Data will be presented based on samples collected at the Belleville, Napanee, Hay Bay, Glenora, and Conway stations in 1975, 1976, 1979, 1980, and 1981 and from Belleville and Conway in 1982 and 1983.

From the very beginning of this study, every effort was made to standardize procedures so that results from year to year would be directly comparable. In 1982 and 1983, decreasing budgets necessitated that samples be collected biweekly instead of weekly and from two stations instead of five, but all other aspects have remained identical since the first samples were collected and enumerated in 1975.

All samples were collected with a 30-L Schindler-type sampler (Schindler 1969) fitted with a 75-μm mesh and bucket and preserved in 10% neutral formalin. At the Belleville and Napanee stations, samples were collected every metre beginning at 1 m to within 1 m of the bottom (usually four samples each cruise) and at Hay Bay every metre in the top 3 m and at the 6- and 8-m levels (five samples per cruise). At Glenora and Conway, samples were taken at the 1-, 3-, 5-, 8-, 10- and 15-m levels at both stations with further samples being taken at 18 m at the Glenora station and at the 20-, 25-, and 30-m levels at Conway. In all production and biomass calculations, species abundances were estimated from depth-weighted means.

The proportion of any species of zooplankton enumerated was dependent on its density. The fraction counted generally ranged from 1/10 at upper bay stations to 1/4 at lower bay stations, but could be smaller or greater when animals were particularly dense or scarce. Subsamples were taken by emptying the entire sample into a beaker, thoroughly mixing, and then pouring out an aliquot into a graduated cylinder. This subsample was then transferred onto a 4 × 6 × 1 cm gridded dish. At least 300 animals in any subsample were enumerated.

To estimate zooplankton production it is necessary to know the rate at which eggs develop in relation to water temperature. For our study we derived egg development curves for several species using the procedure of Cooley (1978) in some cases and literature values for others. A single curve was generated for *Bosmina longirostris* and *Eubosmina coregoni* (as described in Deevey and Deevey 1971) using the eggs of both species indiscriminately. Eggs were incubated at 4, 7, 10, 14, and 23°C, but the final curve was derived from average development times determined at all but the coldest temperature, which was omitted because of excessive mortality. Individual curves were produced for *Chydorus sphaericus* at all of the above temperatures and for *Ceriodaphnia lacustris* from 10 to 23°C as above and also at 27°C.

Literature values were used to derive the same relationship for *Diaphanosoma birgei* and *Daphnia retrocurva*. For the latter, a generalized curve was estimated by using nine different sets of data for *Daphnia* sp. found in the literature (Allan 1977; Geiling 1969; Hall 1964; Korinek 1970; George and Edwards 1974; Munro and White 1975; Elster and Schwoerbel 1970; and Esslova 1959). More data are available for *Daphnia* sp. but these representatives were selected because each set represented a single curve for a particular species. For *Diaphanosoma birgei* a generalized curve was estimated using values found in Elster and Vollenweider (1961) and Gras and Saint-Jean (1969).

Single egg development curves were developed for all cyclopoids and for all calanoids by treating all the eggs as though they were from a single species. This approach was adopted because it was impossible during the enumeration process to speciate the immature instars of the various copepod species found in the Bay of Quinte and because they are numer-

TABLE 1. Egg development curves used in estimating K in equation 1. All curves are expressed as Bělehrádeks' equation $K = a(T - \alpha)^b$, where K = development time in hours, T = temperature, and a, b, and α are fitted constants.

Species or group	Mean individual dry weight used (µm)	Constants equation used in Bělehrádek's equation		
		a	α	b
Bosmina longirostris	1.2	3 750 848	−15.4	−3.11
Eubosmina coregoni	1.8	3 750 848	−15.4	−3.11
Daphnia retrocurva	4.2	65 912	−6.1	−2.12
Ceriodaphnia lacustris	1.9	1 763	3.7	−1.28
Chydorus sphaericus	0.6	138 279	−4.9	−2.43
Diaphanosoma birgei	4.0	1 767	−1.9	−1.08
All cyclopoids	3.3	7 590	−3.4	−1.40
All calanoids	9.0	38 474	−3.7	−2.00

ically of much lesser importance than the cladocerans mentioned previously. We felt it was better to deal with these species as groups in this way rather than ignore them totally. To arrive at a single curve for each species group we first assumed that b in Bělehrádek's equation was −1.4 for cyclopoids and −2.0 for calanoids (Cooley and Minns 1978). We then forced a fit of this equation to available data on egg development rates for species known to exist in the Bay of Quinte. The egg development rate data used in estimating production in this study are summarized in Table 1.

Estimates of population parameters were calculated using the general approach first described by Elster (1954) as modified by Edmondson (1969) for rotifers and corrected by Paloheimo (1974).

More recently, Borgmann et al. (1984) have further modified and refined this approach. The instantaneous rate of reproduction b over an interval can be calculated using Paloheimo's (1974) equation as

$$(1) \qquad b = \frac{\ln\left[\left(\frac{E_0}{N_0} + \frac{E_t}{N_t}\right)/2 + 1\right]}{K/24}$$

where E_0 and E_t are the total number of eggs in the population at the beginning and end, respectively, of an interval of t days, N_0 and N_t are the total number of adults and juveniles, and K is the mean egg development time over the interval based on an estimate of the mean water temperature over the interval. The mean instantaneous rate of population change r over the same interval can be calculated from

$$(2) \qquad N_t = N_0 e^{rt} \text{ or } r = \frac{\ln N_t - \ln N_0}{t}.$$

Once b and r are known, then the mean instantaneous death rate d over the interval can be calculated from

$$(3) \qquad r = b - d.$$

As explained by Borgmann et al. (1984), the total number of animals dying in the interval (i.e. D_t) can be calculated as

$$(4) \qquad D_t = \frac{d}{r}(N_t - N_0) \text{ providing } r = 0.$$

If $r = 0$, then $N_t = N_0$ and D_t is given by

$$D_t = d \cdot N \cdot t \qquad \text{for } r = 0 \text{ over interval } t.$$

In practice, as with Borgmann et al. (1984), we used this equation whenever r was less than 0.005 and set N equal to the mean of N_0 and N_t.

To estimate the production of biomass in interval t (expressed as production lost from the system due to mortality), we multiplied D_t by the mean dry weight w of each individual species (or species group):

$$(5) \qquad P_t = D_t \cdot w.$$

This weight was assumed constant for each species or species group (see Table 1) and was taken from the unpublished data of J. B. Wilson and N. H. F. Watson of our laboratory.

To estimate mean population biomasses B_t for interval t, we multiplied the two successive population estimates N_0 and N_t at the beginning and end of the interval by w (which we assumed to be constant over the year) and averaged them:

$$(6) \qquad B_t = \frac{N_0 + N_t}{2} \cdot w.$$

If the product of B_t and interval length is summed for each interval over the entire season and divided by the length of the season, an estimate of the seasonal mean biomass or B is obtained. If the total seasonal production (in our study, generally from May through September) which is the sum of all P_t is divided by the length of the season we obtain an estimate of the mean daily biomass production or P. The often used P/B coefficient is a production rate expressing the daily addition to existing biomass, in this case averaged over an entire season. The reciprocal of this coefficient is the mean daily turnover time and expresses (assuming B is constant) how long it takes to replace the existing biomass.

For all of the above calculations each population estimate (whether total adults and juveniles or total eggs) was obtained from the mean of three successive sampling dates, a technique whereby the data are "smoothed" to minimize the influence that any single aberrant sampling day might have on overall estimates.

In the above calculations the data were truncated to correct for unrealistic conditions. On occasion, especially when abundances were low, the death rate calculated from equation 3 was negative and for purposes of the remaining calculations was set to 0 (see Table 1). We recognize that a bias is introduced into the estimates of species production doing this, but given the other uncertainties in a variety of assumptions we feel any error introduced is negligible.

To illustrate how population production and biomass estimates are calculated, we offer the following example. In Fig. 2 the population dynamics of *Bosmina longirostris* are illustrated for the Glenora station in 1981. The data illustrated are used to construct a table to estimate production and biomass, as shown in Table 2. In our study, similar tables were prepared for six individual cladoceran species, and for all cyclopoids, and for all calanoids treated as a group as though they were a single species. These tables were calculated for each main sampling station in each of the five years when all stations were sampled and for Belleville and Conway in 1982 and 1983. We believe that these 1982 and 1983 estimates of production are directly comparable with other years of this study even though samples were taken biweekly in these years. We checked for bias by recalculating seasonal production in all years using every other series of zooplankton samples collected, and obtained similar results.

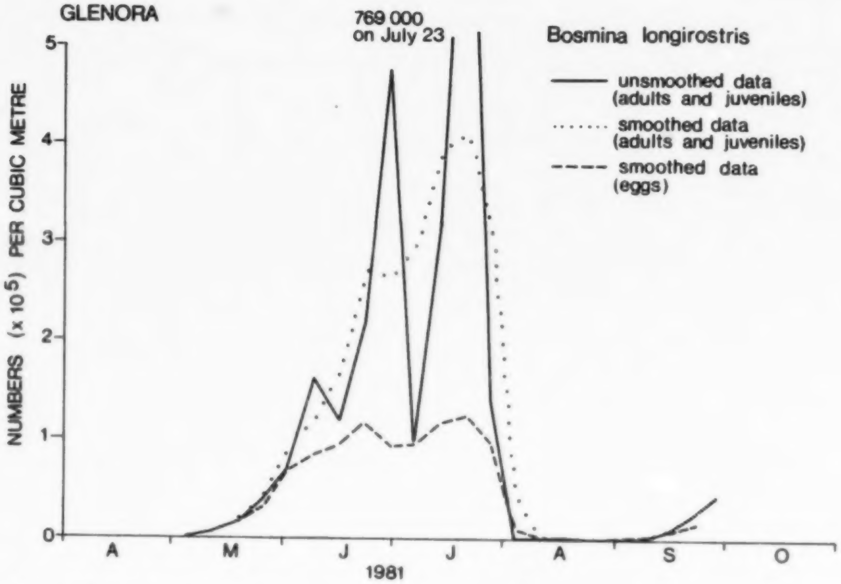

FIG. 2. Population dynamics of *Bosmina longirostris* at Glenora in 1981 used to illustrate how data were "smoothed" prior to calculating production. See also the data summarized in Table 2.

Results

Species Composition

All five stations in all years were dominated numerically by cladocerans (Table 3), in particular by *Eubosmina coregoni*, *Bosmina longirostris*, and *Chydorus sphaericus*. In most samples at any time of the year these three species represent 80% or more of all cladocerans present. If *Daphnia retrocurva*, *Ceriodaphnia lacustris*, and *Diaphanosoma birgei* are included the figure is closer to 99%.

Immature cyclopoid nauplii and copepodites were also abundant in most samples. The numerical importance of cyclopoids was more pronounced in the lower bay where over the course of any season the immature forms accounted for 43% of all animals. The corresponding figure for the upper bay was 82% for cladocerans and 17% for cyclopoids. The remaining 1% of animals were calanoids.

Over the seven years of this study many other species have been found in samples, including six species of *Daphnia*, at least four species of *Ceriodaphnia*, numerous chydorids, eight species of cyclopoids, and eight calanoids including five diaptomids (Table 3).

Species Abundance

The dominance of *Bosmina* and *Eubosmina* in this system is obvious from the data on standing crop, expressed as seasonal mean biomass averaged over the entire sampling season (Fig. 3). These data also show the decreasing proportional abundance of cladocerans going from the upper bay stations of Belleville and Napanee into the lower bay stations of Glenora and Conway and the increasing proportional abundance of cyclopoids. In addition there are no obvious changes in seasonal mean biomass between the two pretreatment years and any of the five post-treatment years. There is a definite gradient of lower overall seasonal mean biomass in every year of study as one moves from the shallow eutrophic upper bay to the deeper mesotrophic lower bay.

The abundance of the three dominants (*Eubosmina*, *Bosmina*, and *Chydorus*) in the Bay of Quinte ecosystem is highly variable from year to year and from station to station (Fig. 4a and 4b). If we assume that Belleville is representative of the upper bay and Conway is representative of the lower bay, it can be seen that in most years at both stations these three species account for most of the cladocera found in the samples. At Conway during all years of this study, *Bosmina longirostris* was overwhelmingly the dominant species from May into August at which time another species may or may not replace it. In 1982 the population of this species exploded in mid-July and continued to dominate samples through most of August. At Belleville the species composition of the three numerical dominants over the seven years of study has been more variable. In one pretreatment year (1976) and one postphosphorus treatment year (1983), *Bosmina longirostris* dominated the species composition in early summer and late fall, respectively. Over three of the other five years of sampling, while common, it was a minor contributor to the overall cladoceran abundance and in 1981 and 1982 it was codominant with *Eubosmina*. Although not shown in Fig. 4a and 4b, we have similar data from the other three cruise stations of Napanee, Hay Bay, and Glenora. Those data are as variable but consistent with what was observed at Belleville and Conway.

The other dominant in this system, *Chydorus sphaericus*, unlike most other species in the Bay of Quinte, is a common open-water inhabitant throughout most of the year including winter. Its abundance at upper bay stations peaks in July and August and slightly later at the cooler lower bay stations.

In 1983, *Daphnia retrocurva* assumed at Belleville a numerical importance unprecedented in any previous year at any other station (Fig. 4a). In mid-June it assumed the role of dominant cladoceran in the system. Following this peak its numbers dropped rapidly, and by mid-August it was a minor constituent of the zooplankton community. Even with this resurgence, overall in 1983 its mean daily abundance was only slightly higher than in 1979 and 1982 and its seasonal production was

TABLE 2. An example to illustrate how annual production is calculated for dominant species in the Bay of Quinte. This example is for ***Bosmina longirostris*** at the Glenora station in 1981.

Date (1981)	No. of anim/L (raw)	No. of anim/L (smooth)	No. of eggs/L (smooth)	b (day^{-1})	r (day^{-1})	$d = b - r$ (day^{-1})	D_t (L^{-1})	B (μg/L)	P (μg/L)
June 3	71.7	etc.							
11	163.8	118.3	85.7						
				0.0587	0.0578	0.00095	0.814	171.5	0.977
17	119.6	167.4	95.4						
				0.0491	0.0694	0.0[a]	0.0	263.7	0.0
24	218.9	272.1	117.6						
				0.0513	−0.0035	0.0548	104.4	322.7	125.3
July 1	478.0	265.5	94.0						
				0.0708	0.0172	0.5365	106.0	339.1	127.2
8	99.9	299.5	95.7						
				0.0721	0.0401	0.0320	77.4	417.7	92.9
15	320.7	396.5	117.7						
				0.0746	0.0052	0.06945	225.0	485.9	269.9
23	769.0	413.2	124.5						
				−0.0993	−0.0425	0.1418	354.9	432.1	425.8
30	150.0	306.8	97.5						
				0.0934	−0.2995	0.3929	335.8	214.6	402.9
Aug. 5	1.4	50.9	10.4						
12	1.1	etc.							

NOTE: mean individual dry weight assumed to be 1.2 μg.

[a] Because calculated $b - r$ is less than 0.005, d is set at 0.

	Summary by month		
	Production		
	Total (μg/L)	Mean (μg·L^{-1}·d^{-1})	Mean biomass (μg/L)
May	0	0	37.3
June	141.2	4.7	201.9
July	1000.9	32.3	411.2
Aug.	413.9	13.4	42.8
Sept.	17.5	0.8	10.5
Total	1573.5		

NOTE: For this example, production was estimated over an interval that began on May 12 (day 132) and ended on September 23 (day 266).
Total interval length = 266 − 132 = 134 d.
Mean daily production/seasonal mean biomass = 1573.5/134/157.3 = 0.075 or mean daily turnover rate = 13.3 d.
Seasonal mean biomass is calculated from $\Sigma B \cdot t/\Sigma t$ = 21079.3/134 = 157.3 μg/L.

actually less than in those years while only slightly above 1975.

Although *Daphnia galeata mendotae* is not considered a dominant in this ecosystem its abundance appears to have responded positively to the control of phosphorus (Table 4). At Belleville and Napanee its abundance has increased on average approximately 15 and 35 times, respectively, in the years of postphosphorus control. The smaller increases in the lower bay are most likely related to some increase in recruitment from the upper stations.

Species Contribution to Production

Over the seven sampling years, the relative contribution of each species to overall seasonal production is similar to the relative contribution to seasonal mean biomass (Fig. 5). In the first three years (1979–81) following phosphorus control there appeared to be a slight drop in overall production by the macrozooplankton in the upper bay stations of Belleville and possibly Napanee (Table 5). The lower bay stations of Glenora and Conway showed no obvious trend, which was expected since the overall water quality including phosphorus levels of these stations changed little if at all following phosphorus control (Robinson 1986). In 1982 and 1983 the total seasonal production appears to have increased substantially at Belleville (Fig. 5). This occurred at a time when the water quality at Belleville was still improving (Robinson 1986). In these same two years, seasonal production was also increasing in the lower bay station of Conway where the primary production and chlorophyll (Millard and Johnson 1986) and total phosphorus concentrations (Robinson 1986) have remained unchanged from pretreatment years.

In the upper bay, at Belleville and Napanee, *Bosmina* and *Eubosmina* together contributed from 41 to 72% with an average of approximately 61% at both stations over the period of this study. There is no discernible change in pre- and post-treatment years. However, in any given year the individual contribution by either species was substantial.

There appears to be a relationship between the dominance of these two species relative to each other and possibly to trophy (Fig. 5). Generally when *Eubosmina*'s contribution to total pro-

TABLE 3. Relative abundance of limnetic macrozooplankton species found in the Bay of Quinte during the period of study (1975–83) (1, numerical dominant; 2, common; 3, rare or absent in some years).

Species	Relative abundance
Cladocerans	
Bosmina longirostris	1
Eubosmina coregoni	1
Daphnia retrocurva	1–2
Daphnia longiremis	2
Daphnia galeata medotae	2
Daphnia pulex	2
Daphnia ambigua	3
Daphnia catawba	3
Ceriodaphnia lacustris	1–2
Ceriodaphnia quadrangula	3
Ceriodaphnia sp.	3
Chydorus sphaericus	1
Diaphanosoma birgei	1–2
Diaphanosoma sp.	3
Holopedium gibberum	2–3
Alona guttata	2
Sida crystallina	3
Polyphemus pediculus	3
Leptodora kindtii	2
Cyclopoids	
Cyclops bicuspidatus thomasi	1
Cyclops vernalis	2–3
Cyclops scutifer	3
Tropocyclops prasinus mexicanus	1
Mesocyclops edax	1
Eucyclops agilis	2
Eucyclops speratus	3
Calanoids	
Limnocalanus macrurus	2–3 (lower bay only)
Diaptomus sicilis	2–3 (lower bay only)
Diaptomus oregonensis	2
Diaptomus siciloides	2
Diaptomus minutus	2
Diaptomus ashlandii	2–3
Eurytemora affinis	2
Epischura lacustris	2–3

duction is strong *Bosmina* will be weak as in 1975 and 1980 at Belleville. The reverse was true at Conway in 1976 and 1980 and at Glenora in 1976. *Eubosmina* in the upper bay never accounted for less than 23% of the total seasonal production with means of 42 and 33%, respectively, at Belleville and Napanee. In the mesotrophic lower bay stations the means were 20 and 13% at Glenora and Conway, respectively, and *Eubosmina* rarely accounted for more than 20% of the total production.

After *Eubosmina* and *Bosmina*, *Daphnia retrocurva* is the next major contributor to overall production in the bay. This is in spite of *Chydorus*'s numerical superiority in most years at most stations and results from the fact that *Daphnia retrocurva* is on average seven times heavier than *Chydorus* (Table 1). *Daphnia*'s contribution to seasonal production is also variable from year to year and station to station. At Belleville the range was 13–42% with an average of 22%. At all other stations the range was 5–26% with an overall average near 14%.

Chydorus contributed little to overall production in this system despite its large numbers. The relative contribution to total production was related to trophy. In the mesotrophic lower bay the total contribution was always near 1 or 2%. In the midbay it was 3–7% and in the upper bay it varied from 4 to 11% at Belle-

TABLE 4. Mean seasonal abundance (numbers/m³) of *Daphnia galeata mendotae* in the Bay of Quinte. The mean seasonal abundance is a time-weighted average calculated by dividing the area under the curve of abundance plotted against time and dividing by the length of the sampling season.

	Pretreatment		Post-treatment				
Station	1975	1976	1979	1980	1981	1982	1983
Belleville	286	3	513	4356	813	5454	2179
Napanee	44	51	585	3036	1798	—	—
Hay Bay	44	51	187	2295	560	—	—
Glenora	33	9	468	350	50	—	—
Conway	79	3	315	104	25	41	247

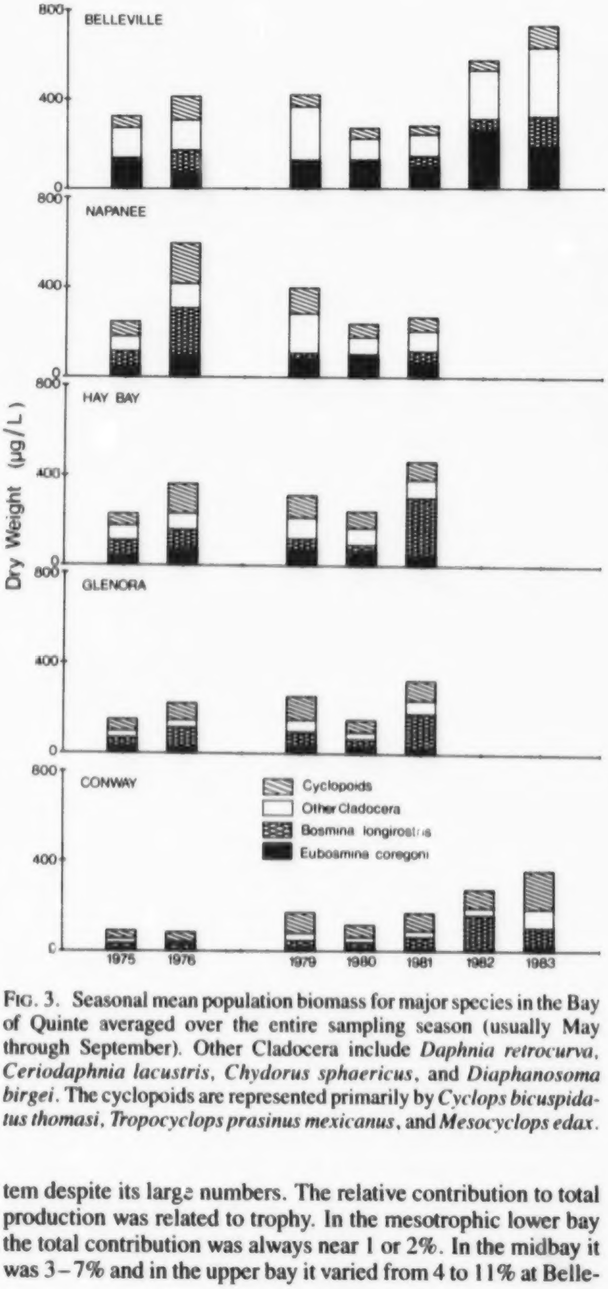

FIG. 3. Seasonal mean population biomass for major species in the Bay of Quinte averaged over the entire sampling season (usually May through September). Other Cladocera include *Daphnia retrocurva*, *Ceriodaphnia lacustris*, *Chydorus sphaericus*, and *Diaphanosoma birgei*. The cyclopoids are represented primarily by *Cyclops bicuspidatus thomasi*, *Tropocyclops prasinus mexicanus*, and *Mesocyclops edax*.

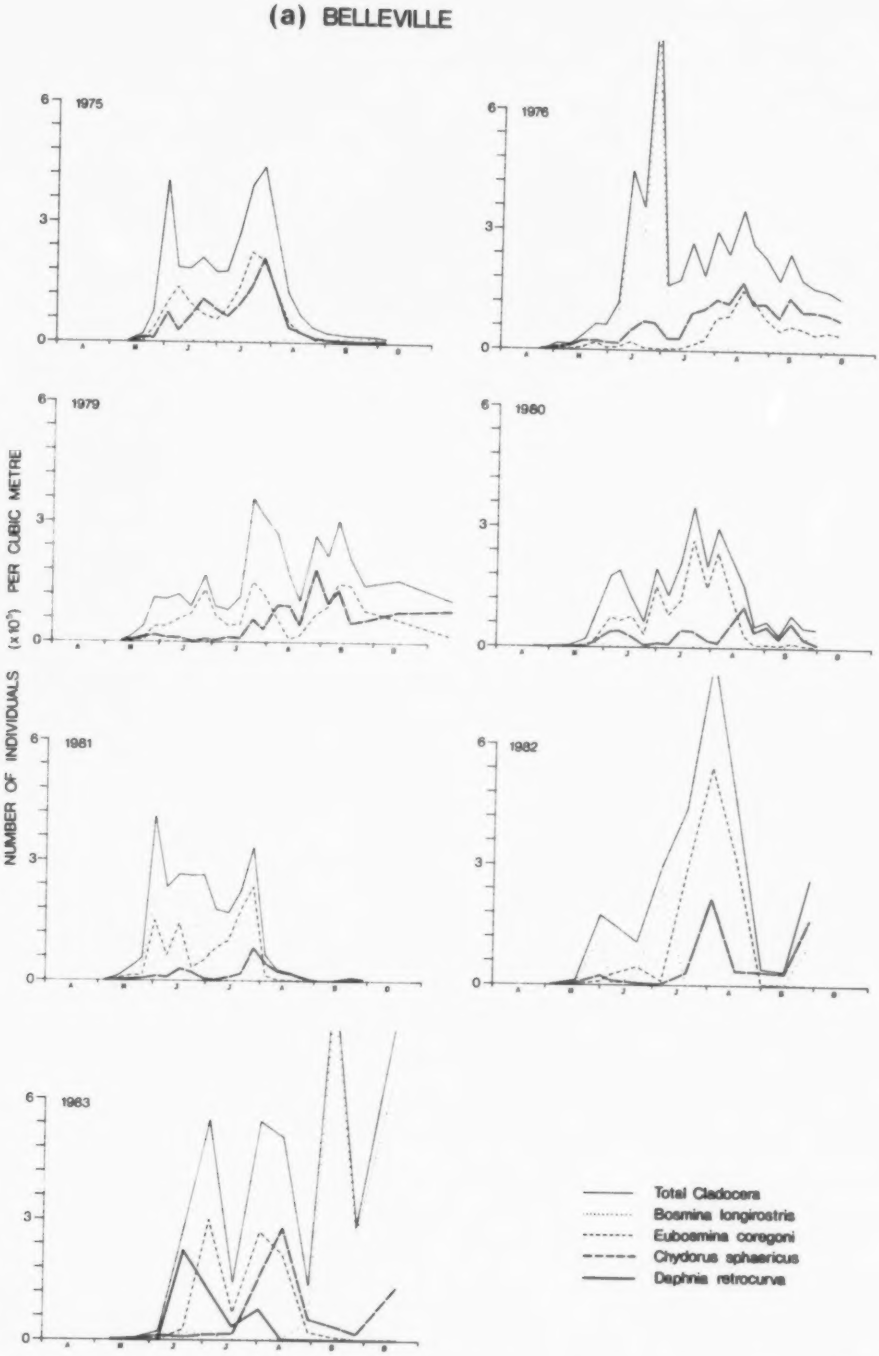

FIG. 4. Population dynamics for major macrozooplankton species at (a) Belleville and (b) Conway in the Bay of Quinte. *Daphnia retrocurva* is included at Belleville for 1983 only. These curves have been plotted using "unsmoothed" data.

ville with an average of 6% and from 7 to 9% at Napanee.

The other two common cladocerans, *Ceriodaphnia lacustris* and *Diaphanosoma birgei*, consistently played a minor role in the system and in most years at most stations accounted for 10% or less of the total seasonal production as did the cyclopoids in the upper and midbay sections. In the lower bay the cyclopoids played a greater proportional role in production occasionally accounting for 15–20% of the total. Calanoids never accounted for more than 4% at any station in any year and in the upper bay often represented less than 1% of the seasonal production.

Mean Daily Turnover Times

The P/B coefficient we have calculated is a seasonal mean and indicates the daily addition to existing biomass. The inverse of this coefficient gives an estimate of the time in days required

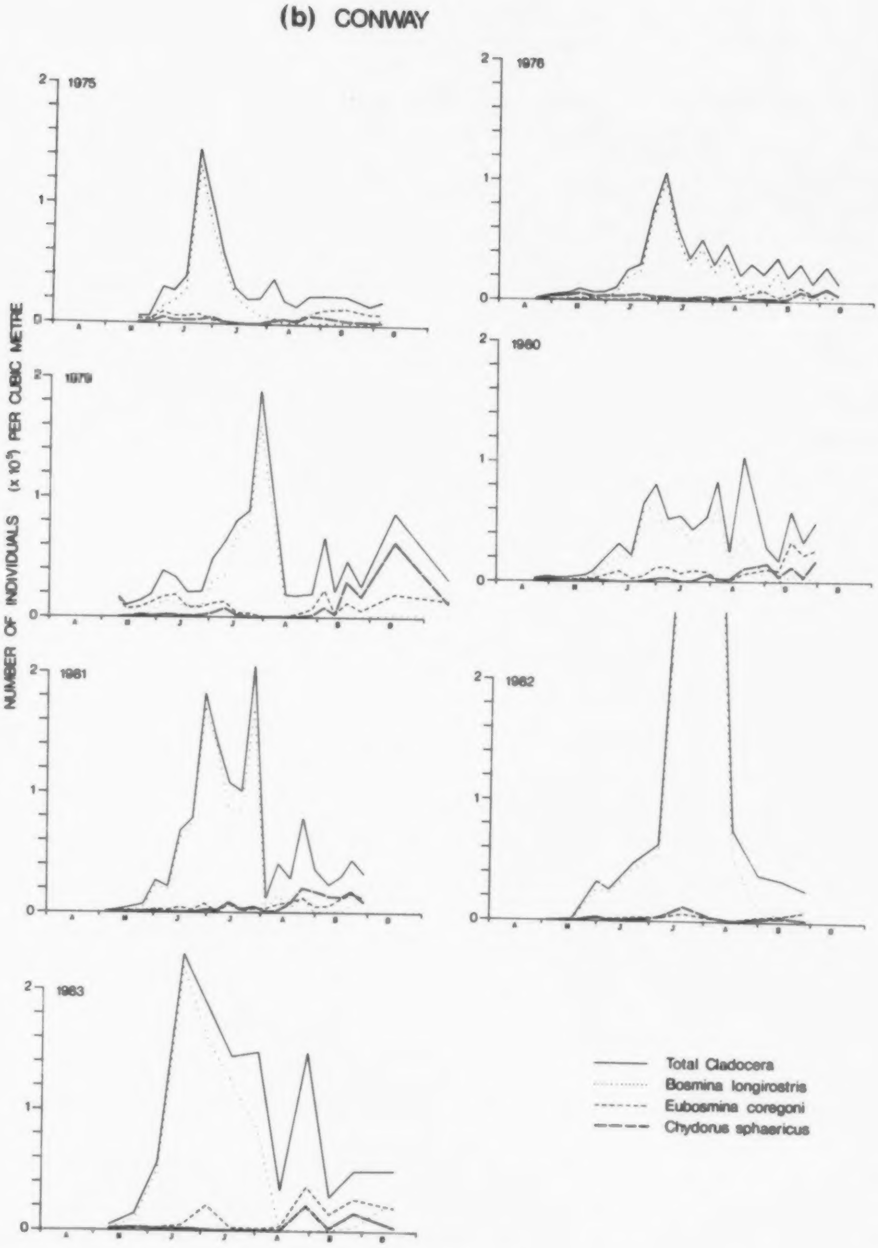

FIG. 4. (*Concluded*)

for the population to replace its biomass on average over the season from May to September. We have further averaged these times over the seven years of this study (Table 6) for the six dominant cladocerans in the Quinte ecosystem. These clearly reflect a gradient of increasing turnover times for each species as one travels from the shallow warmer and more eutrophic upper bay to the Conway station. Both *Eubosmina* and *Bosmina* more than double their times whereas *Daphnia retrocurva* has only a 44% increase from the Belleville to the Glenora station. The shortest turnover times are found with *Ceriodaphnia* and the slowest with *Diaphanosoma*. Most species show great similarity in times at the two upper and at the two lower stations with the midbay station of Hay Bay between these two extremes.

Discussion

When we became involved in the zooplankton sampling part of Project Quinte in 1975, we, like others in the group, had expectations as to how the system would respond to the phosphorus reductions. We recognized that reduced chlorophyll levels were likely, but would they be low enough to cause a shift in species composition and abundance? Would the continued contribution of phosphorus in the sediments of the upper bay stations negate any overall reductions from point source loadings and for how long? Fish populations were likely to respond to phosphorus reductions which could in turn dramatically alter zooplankton composition because of the changes in predatory

TABLE 5. Estimates of the percent contribution to seasonal production[a] (May through September) for major species or groups of species in the Bay of Quinte ecosystem. Total seasonal production is expressed as μg / dry wt. / L. Samples were collected weekly at all stations from 1975 to 1981 and biweekly in 1982 and 1983. A lack of data indicates no sampling done. Species or group codes: 1. *Bosmina longirostris*; 2. *Eubosmina coregoni*; 3. *Daphnia retrocurva*; 4. *Ceriodaphnia lacustris*; 5. *Chydorus sphaericus*; 6. *Diaphanosoma birgei*; 7. all cyclopoids; 8. all calanoids.

Station	Year	Group 1	2	3	4	5	6	7	8	Seasonal production
Belleville (upper bay), mean depth = 5.2 m	1975	3	61	21	1	9	2	2	<1	8 866
	1976	30	31	15	7	11	1	4	1	8 332
	1979	<1	42	42	2	4	4	6	2	6 609
	1980	2	64	19	1	5	3	5	1	6 174
	1981	19	48	17	4	5	2	4	2	5 702
	1982	7	52	25	2	4	<1	5	3	13 286
	1983	24	45	13	5	5	3	5	<1	15 122
Napanee (upper bay), mean depth = 5.4 m	1975	43	29	6	6	8	7	2	<1	5 821
	1976	46	23	5	9	7	1	9	<1	10 275
	1979	13	28	26	11	8	1	11	<1	6 093
	1980	9	49	21	3	8	2	7	1	3 901
	1981	27	34	16	4	9	2	8	1	4 781
	1982									
	1983									
Hay Bay (midbay), mean depth = 11.5 m	1975	35	27	17	7	7	2	2	3	3 918
	1976	40	28	12	5	6	<1	8	1	4 757
	1979	14	23	14	7	5	2	11	1	3 486
	1980	19	35	20	3	8	3	10	2	2 661
	1981	54	14	13	5	7	1	5	1	6 233
	1982									
	1983									
Glenora (lower bay), mean depth = 21.5 m	1975	36	28	15	7	4	1	6	3	1 676
	1976	60	20	7	4	4	<1	4	1	2 117
	1979	33	20	20	4	1	2	16	2	2 205
	1980	29	21	19	4	6	1	17	4	1 311
	1981	48	12	10	12	3	2	12	2	3 289
	1982									
	1983									
Conway (lower bay), mean depth = 32.3 m	1975	38	20	20	11	2	1	7	2	940
	1976	56	14	14	6	2	<1	9	1	798
	1979	25	16	24	6	1	1	25	3	1 216
	1980	29	16	21	6	2	1	21	3	1 068
	1981	38	10	17	8	2	1	21	2	1 633
	1982	67	2	12	13	<1	<1	5	<1	2 224
	1983	27	10	23	15	1	1	22	1	3 315

[a] Seasonal production is almost identical to total annual production in this instance, since abundances and water temperatures are low in months before May and after September.

TABLE 6. Mean daily turnover times expressed in days for the six dominant cladocerans in the Bay of Quinte. The mean for all cladocerans is weighted by the relative contribution to total biomass and production for each of the six species represented here.

Station	*Bosmina longirostris*	*Eubosmina coregoni*	*Daphnia retrocurva*	*Ceriodaphnia lacustris*	*Chydorus sphaericus*	*Diaphanosoma birgei*	All cladocerans
Belleville[a]	5.0	4.3	7.7	3.5	6.7	11.1	5.6
Napanee	5.0	5.3	7.7	4.2	7.7	12.5	5.9
Hay Bay	6.0	7.1	9.1	4.4	19.0	10.0	8.3
Glenora	11.1	9.1	11.1	5.6	14.3	14.3	11.1
Conway[a]	11.1	9.1	9.1	5.0	14.3	16.7	10.0

[a] Averaged over 7 yr; all others were averaged over 5 yr.

pressure. We suspected that the ultimate response to reduced phosphorus would be lower overall zooplankton production and standing crop and changes in species composition.

Five years after the 1978 phosphorus reductions were implemented, our results show none of the above trends. There are a number of observations that merit attention possibly because they are the forerunners of changes that will be more significant in the future.

The association of *Bosmina* and *Eubosmina* in this system is variable and unpredictable. In most years, as expected, *Eubosmina* does better in the shallow eutrophic upper bay stations of Belleville and Napanee than does *Bosmina* whereas in the mesotrophic deeper lower bay, *Bosmina* is always dominant. However, in some years at both upper bay stations the two

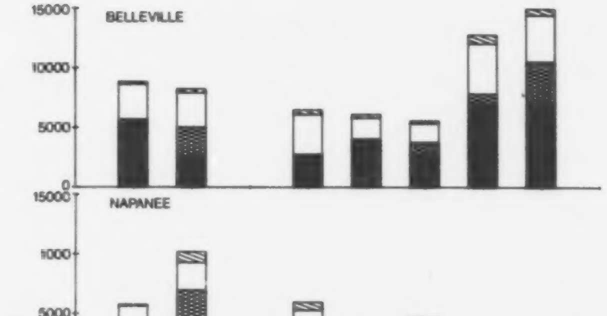

FIG. 5. Total seasonal production (May to September) expressed as dry weight for macrozooplankton in the Bay of Quinte.

species have contributed equally or *Bosmina* has actually done better. Therefore the morphometric differences alone between the upper and lower bay stations cannot always account for the relative dominance of these two similar species.

In one instance the two dominated the system at different times of the year, indicating a temporal separation which would reduce direct competition. But in another year (1981, Napanee) the two had coincident abundance curves for most of the year. In addition, the upper bay affords little opportunity for a spatial separation, since it is shallow and never stratifies.

We expect that *Chydorus* will become less abundant if the upper bay becomes less eutrophic. *Chydorus* is a "classic" indicator of cultural eutrophication. Normally it is found near the bottom, but often appears in large numbers during blooms of blue-green algae which provide it with food and substrate. Many feel it is not a true member of the plankton (Brooks 1969). In the Bay of Quinte it is commonly found in open water all year, including winter, and does tend to peak in the latter part of July and into August when blue-greens become most abundant. On occasion, we recorded its numbers expanding to record seasonal levels in September, near the end of our routine sampling season. As of the 1983 sampling season there is no indication of a trend towards less *Chydorus* in the upper bay even though blue-greens have declined in response to lower phosphorus levels (Nicholls et al. 1986).

The apparent resurgence of *Daphnia galeata mendotae* in the upper Bay following phosphorus treatment was unexpected. This *Daphnia* species is large (with a mean dry weight of approximately 19.5 µg) and should experience heavy predatory pressure in the Bay of Quinte because planktivores abound. The possible causes of this resurgence and its permanency are unknown at this time. While the recent success of this species is measurable, it must be remembered that its seasonal abundance on average is still below that of the six dominant cladocerans listed in Table 1. At this point we can only postulate that this is an indication that some changes in the predatory community may have occurred.

It was expected that seasonal mean turnover times would increase from the upper to the lower bay because temperatures are on average 4 or 5° warmer (Robinson 1986) in the shallower, unstratified water during the more productive June to August growing season. Our data indicate that the three numerically dominant cladocerans, *Eubosmina*, *Bosmina*, and *Chydorus*, in the most eutrophic water are also the three species which have the greatest proportional increase in turnover times in the lower bay. Each of these three species has a turnover time in the lower bay more than double that at the Belleville station. The increase seems greater than what could be expected simply by a 4 or 5° change in temperature, especially since the other three dominants exhibit an increase in their turnover times from 18 to 50%. These data tend to support the concept, not surprisingly, that some zooplankton are better suited to exploit certain trophic conditions than are others. Our data on turnover times are consistent with the hypothesis that *Bosmina*, *Eubosmina*, and *Chydorus* are more productive on average in the more eutrophic environments than are the other three cladoceran dominants in the system.

Another uncertainty that influences our ability to interpret the zooplankton data is the lack of quantified information on zooplankton predators. The apparent increases in secondary production in the last few years could well be related to reduced predation by planktivores and other invertebrate predators. Planktivores can dramatically alter zooplankton production (Brooks and Dodson 1965; Wells 1970; O'Brien 1979) and could significantly mask changes related to reduced primary production caused by nutrient control.

In summary, while there have been significant and measurable changes in the Bay of Quinte ecosystem following phosphorus treatment to the water quality, phytoplankton, and fish communities, no such obvious changes have occurred in the macrozooplankton. Even if the water quality in the upper Bay of Quinte continues to improve and approaches that of the lower bay, it will still be dominated by small-bodied cladocerans such as *Bosmina*, *Eubosmina*, and *Chydorus*. There may be an increase in the representation by copepods, but in the foreseeable future we expect no substantial change in this community.

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References

Allan, J. D. 1977. An analysis of seasonal dynamics of a mixed population of *Daphnia* and the associated cladoceran community. Freshwater Biol. 7: 505–512.

Borgmann, U., H. Shear, and J. Moore. 1984. Zooplankton and potential fish production in Lake Ontario. Can. J. Fish. Aquat. Sci. 41: 1303–1309.

Brooks, J. L. 1969. Eutrophication and changes in the composition of the zooplankton. *In* Eutrophication causes, consequences, and correctives. National Academy of Sciences, Washington, DC. 661 p.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of zooplankton. Science (Wash., DC) 150: 28–35.

Cooley, J. M. 1978. The effect of temperature on the development of diapausing and subitaneous eggs in several freshwater copepods. Crustaceana 35: 27–34.

Cooley, J. M., and C. K. Minns. 1978. Prediction of egg development times of freshwater copepods. J. Fish. Res. Board Can. 35: 1322–1329.

Deevey, E. S., and G. B. Deevey. 1971. The American species of *Eubosmina* Seligo (Crustacea, Cladocera). Limnol. Oceanogr. 16: 201–218.

Edmondson, W. T. 1969. Cultural eutrophication with special reference to Lake Washington. Mitt. Int. Ver. Limnol. 17: 19–32.

Elster, H. J. 1954. Über die Populationsdynamik von *Eudiaptomus gracilis* sars und *Heterocope borealis* Fischer im Bodensee – Obersee. Arch. Hydrobiol. Suppl. 20: 546–614.

Elster, H. J., and J. Schwoerbel. 1970. Beitrage zur Biologie und Populationsdynamik der Daphnien im Bodensee. Arch. Hydrobiol. 38: 18–72.

Elster, H. J., and R. A. Vollenweider. 1961. Beitrage zur Limnologie Agyptens. Arch. Hydrobiol. 57: 241–343.

Esslova, M. 1959. Embryonic development of parthogenic eggs of *Daphnia pulex*. English summary. Vestn. Cesk. Spol. Zool. 23: 80–88.

Geiling, W. T. 1969. Zooplankton production in a series of strip-mine lakes. Ph.D. thesis, University of Missouri, Columbia, MO.

George, D. G., and R. W. Edwards. 1974. Population dynamics and production of *Daphnia hyalina* in a eutrophic reservoir. Freshwater Biol. 4: 445–465.

Gras, R., and L. Saint-Jean. 1969. Biologie des crustaces du Lac Tchad. I. Durées de développement embryonnaire et post-embryonnaire: premiers résultats. Cah. ORSTOM Ser. Hydrobiol. Vol. III: 43–60.

Hall, D. J. 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecology 45: 94–112.

Hurley, D. A. 1986. Effect of nutrient reduction on the diets of four fish species in the Bay of Quinte, Lake Ontario, p. 237–246. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish Aquat. Sci. 86: 270 p.

Johnson, M. G., and D. A. Hurley. 1986. Overview of Project Quinte — 1972–1982, p. 1–6. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Korinek, V. 1970. The embryonic and postembryonic development of *Daphnia hyalina* Leydig (Crustacea, Cladocera) from Lake Maggiore. Mem. Ist. Ital. Idrobiol. 26: 85–95.

Millard, E. S., and M. G. Johnson. 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82. p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81. p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Munro, I. G., and R. W. G. White. 1975. Comparison of the influence of temperature on the egg development and growth of *Daphnia longispina* O.F. Muller (Crustacea: Cladocera) from two habitats in southern England. Oecologia 20: 157–165.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

O'Brien, W. J. 1979. The predator–prey interaction of planktivorous fish and zooplankton. Am. Sci. 67: 572–581.

Paloheimo, J. E. 1974. Calculation of instantaneous birth rate. Limnol. Oceanogr. 19: 692–694.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Schindler, D. W. 1969. Two useful devices for vertical plankton and water sampling. J. Fish. Res. Board Can. 26: 1948–1955.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556–565.

Changes in Abundance and Species Composition in Benthic Macroinvertebrate Communities of the Bay of Quinte, 1966–84

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Johnson, M. G., and O. C. McNeil. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–84, p. 177–189. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

A general decline occurred in numbers and biomass of oligochaetes, sphaeriids, isopods, and, to a lesser extent, chironomids in the Bay of Quinte and adjacent Lake Ontario between 1977 and 1984. This was probably related to a decline in productivity of the bay in response to phosphorus input reductions. The amphipod *Pontoporeia hoyi* declined in the mid-1970s and recovered in the lower bay after 1977 following the collapse of a white perch (*Morone americana*) population. A coincident increase in yellow perch (*Perca flavescens*) may have suppressed numbers of the amphipod *Gammarus fasciatus*, and possibly the isopod *Caecidotea racovitzai*. Changes in chironomid associations included declines in *Chironomus anthracinus* and *C. plumosus* in the lower bay and an increase in *C. atritibia*, a species less tolerant of eutrophic conditions. Changes in oligochaete associations included declines of pollution-tolerant *Limnodrilus hoffmeisteri*, *Tubifex tubifex*, and *Quistadrilus multisetosus* throughout the bay and the increase of *Spirosperma ferox* and of *Stylodrilus heringianus*, a clean-water form found earlier only in adjacent Lake Ontario. Numbers of several species of *Aulodrilus* and *Potamothrix* usually declined. Most sphaeriid species decreased in numbers. Many species shifts were the reverse of those often observed coincident with deteriorating water quality. Species associations changed less in Lake Ontario and the lower bay toward the mouth and more so toward the middle and upper bay.

Il y a eu, entre 1977 et 1984, une baisse générale de la quantité et de la biomasse d'oligochètes, de sphaeriidés, d'isopodes et, à un moindre degré, de chironomidés dans la baie de Quinte et dans la partie adjacente du lac Ontario. Ce phénomène était probablement lié à une baisse de la productivité de la baie suite aux mesures de réduction des apports de phosphore. La population de l'amphipode *Pontoporeia hoyi* a diminué au milieu des années 70 et s'est rétablie après 1977 dans la partie inférieure de la baie, après la disparition d'une population de bars-perches (*Morone americana*). Une augmentation simultanée du nombre de perchaudes (*Perca flavescens*) pourrait avoir entrainé l'élimination d'un certain nombre d'amphipodes de l'espèce *Gammarus fasciatus* et possiblement d'isopodes de l'espèce *Caecidotea racovitzai*. Parmi les changements survenus dans les associations de chironomidés, mentionnons une diminution du nombre de *Chironomus anthracinus* et de *C. plumosus* dans la partie inférieure de la baie et une augmentation du nombre de *C. atritibia*, espèce qui tolère moins les conditions eutrophes. En ce qui concerne les associations d'oligochètes, il y a eu une baisse du nombre de *Limnodrilus hoffmeisteri*, de *Tubifex tubifex* et de *Quistadrilus multisetosus*, espèces qui tolèrent la pollution, dans toute la baie et une augmentation du nombre de *Spirosperma ferox* et de *Stylogrilus heringianus*, forme vivant en eau propre qu'on ne trouvait auparavant que dans la partie adjacente du lac Ontario. Le nombre d'individus de plusieurs espèces d'*Aulodrilus* et de *Potamothrix* a généralement diminué de même que la population de la plupart des espèces de sphaeriidés. De nombreux changements survenus au niveau des espèces ont été contraires à ceux qu'on observe souvent lorsque la qualité de l'eau se détériore. Les associations d'espèces ont moins changé dans le lac Ontario et dans la partie inférieure de la baie, vers l'entrée de celle-ci, mais elles ont changé davantage du côté de la partie médiane et de la partie supérieure de la baie.

Introduction

Extensive eutrophication of the lower Great Lakes by man led to prescriptions for reduction in phosphorus loadings by the Canada–U.S. Great Lakes Water Quality Agreement of 1972 (extended in 1978). Scientists from several agencies and universities collaborated to examine responses to phosphorus reduction in the Bay of Quinte, Lake Ontario (Johnson and Hurley 1986), commencing in 1972.

As part of this study, changes in benthic macroinvertebrate communities in an area of improving water quality were assessed. While macroinvertebrate communities change predictably in worsening eutrophic conditions (Johnson and Matheson 1968; Brinkhurst et al. 1968; Carr and Hiltunen 1965; Cook and Johnson 1974; Johnson and Brinkhurst 1971a), the response to reductions in phosphorus load has received considerably less study. We were interested in whether trends in species composition with improving water quality would be the reverse of trends observed as water quality deteriorated. However, changes in macroinvertebrate communities might be delayed by lagging changes in the benthic subenvironment. Also, if significant shifts occurred in fish communities (for example, a reduction in populations of benthic invertebrate feeders), significant changes in macroinvertebrates might result with little direct relationship to trends in abiotic factors. In fact, a relationship between populations of the amphipod *Pontoporeia hoyi* and white perch (*Morone americana*) became evident, although deterioration of water quality had been suspected initially as the main factor responsible for the decline in *P. hoyi*. This interaction was one of the primary findings in this study.

Benthic macroinvertebrate associations, rates of production, and benthic community metabolism in the Bay of Quinte and

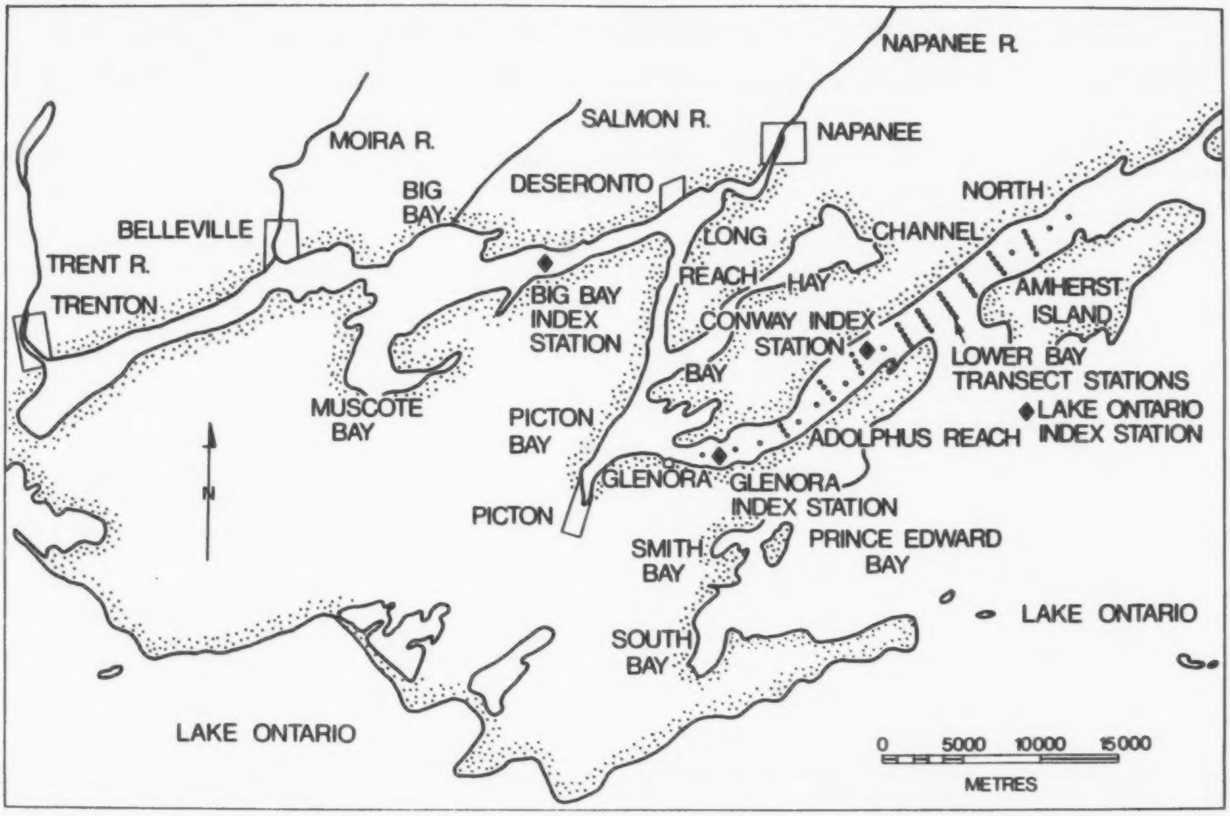
NAPANEE R.
SALMON R.
NAPANEE
MOIRA R.
BIG BAY
DESERONTO
NORTH
BELLEVILLE
LONG REACH
CHANNEL
TRENT R.
HAY
TRENTON
BIG BAY INDEX STATION
CONWAY INDEX STATION
AMHERST ISLAND
BAY
LOWER BAY TRANSECT STATIONS
MUSCOTE BAY
PICTON BAY
LAKE ONTARIO INDEX STATION
ADOLPHUS REACH
GLENORA
GLENORA INDEX STATION
N
PICTON
SMITH BAY
PRINCE EDWARD BAY
LAKE ONTARIO
SOUTH BAY
LAKE ONTARIO
0 5000 10000 15000
METRES

FIG. 1. Locations of 4 index stations (Big Bay, Glenora, Conway, and Lake Ontario) and 52 transect stations in the lower Bay of Quinte (Adolphus Reach and the mouth of the bay). The upper bay, as used in this benthos study, is from Trenton to Deseronto, the middle bay extends to Glenora, and the lower bay is from Glenora to Amherst Island.

adjacent Lake Ontario had been described for the period 1966–68 (Johnson and Brinkhurst 1971a, 1971b). At that time, water quality in the bay was poor because of high phosphorus loadings and a series of years with relatively low flushing rates (Johnson and Owen 1971; Johnson 1986). Walleye (*Stizostedion vitreum*) had declined to extremely low numbers, while white perch and alewife (*Alosa pseudoharengus*) populations were expanding (Hurley 1986).

Further examination of Quinte benthic macroinvertebrate communities was carried out as part of Project Quinte during the period 1972–84 as phosphorus inputs were being reduced (Johnson 1986). The four stations where macroinvertebrate production was measured in 1967–68 together with a new set of transect stations in the lower bay (Adolphus Reach) were employed to assess trends in species composition, biomass, and distributions. The transect stations in the lower bay were established primarily to follow distribution and abundance of the amphipod *P. hoyi*, a significant member of the community because of its importance in diets of fish (Hurley 1986) and its decline in the lower bay by 1972.

With respect to the chronology of phosphorus removal, the 1967 and 1968 benthos study was carried out before any measures were implemented. In 1972, phosphorus reduction in detergents was legislated. By 1978, targets for phosphorus removal were met at wastewater treatment plants (see Minns et al. 1986 and Johnson 1986 for trends in phosphorus inputs and water quality in the Bay of Quinte).

Methods

Collection, sorting, and identification of macroinvertebrates were done in the same way in 1972–84 as in the 1966–68 studies (Johnson and Brinkhurst 1971a). The same 22.5 × 22.5 cm modified Ekman dredge was used throughout, and samples were screened through 0.6-mm-aperture brass screens. Sampling was done in August, which ensured that age 0+ *P. hoyi* were collected quantitatively. The Big Bay, Glenora, Conway, and Lake Ontario stations, which were established for the 1966–68 study, are called index stations; the new lower bay stations are called transect stations (Fig. 1). All four index stations and at least 20 of the 52 transect stations were sampled on every occasion. Six dredge samples were taken on every occasion at index stations and one or two at transect stations. The data base for the period 1972–84 derives from about 550 Ekman samples, while the intensive study in 1966–68 was based on approximately 600 samples. All taxonomic nomenclature was reviewed and standardized.

Data on temperature and oxygen at 1 m over bottom at transect stations, reported by Minns and Johnson (1986), permit comparison of mean and minimum oxygen concentrations among most years for which macroinvertebrate data were available, specifically 1967 and 1968, 1972, 1974–77, and 1982.

Similarity among years at the index stations, in terms of numerical abundance by taxa, was assessed using the "percentage similarity of community" (PSC) (Johnson and Brinkhurst

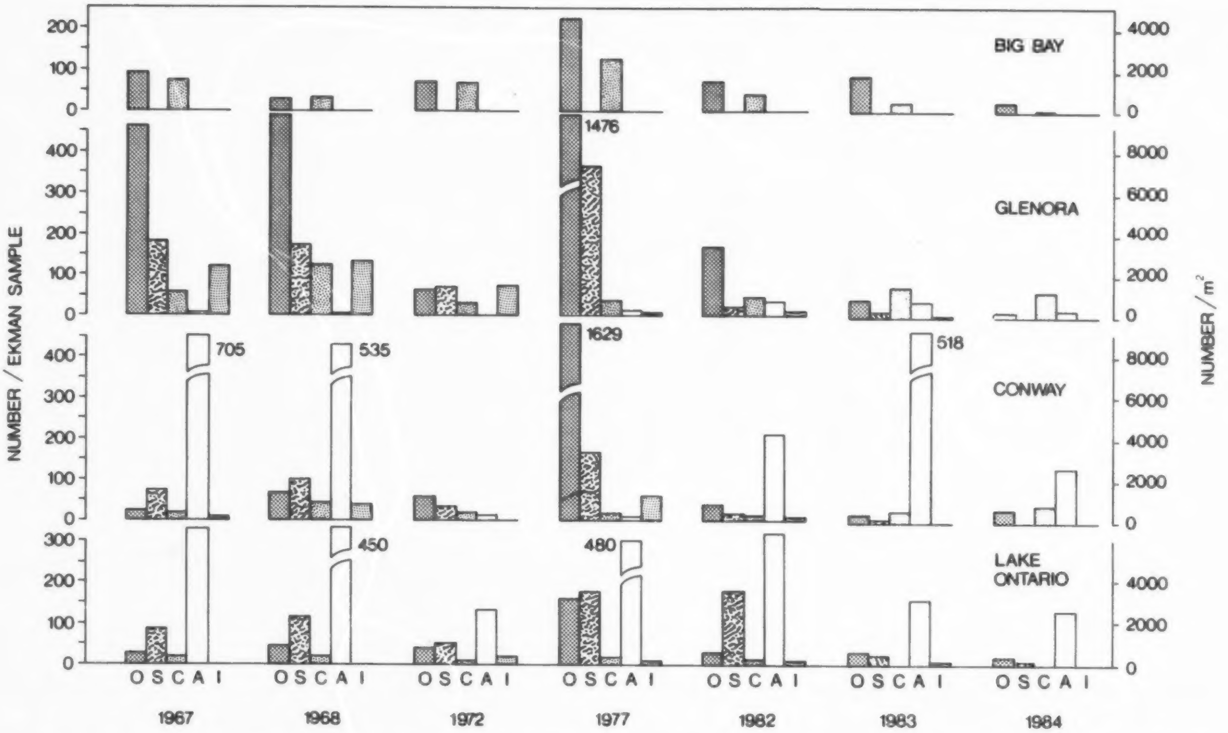

FIG. 2. Mean numbers of individuals of major macroinvertebrate groups collected at the index stations in August of 1967, 1968, 1972, 1977, 1982, 1983, and 1984. Six Ekman samples comprise each data set. Groups are as follows: O, oligochaetes; S, sphaeriids; C, chironomids; A, amphipods; I, isopods.

1971a; Sanders 1960), calculated as

$$\mathrm{PSC} = 100 - 0.5\,|a' - b'| = \sum \min(a', b')$$

in which a' and b' are, for each species, the respective percentages of the total animals in samples A and B. PSC takes values between 0 and 100, which represent the lowest and highest affinity respectively between two samples. Six Ekman samples in each series were compared with the corresponding sample of other series to provide six values of PSC for each comparison. Confidence limits ($P = 0.05$) on the mean values of PSC allowed determination of minimum and maximum probable values of PSC. The years compared were 1967, 1968, 1972, 1977, 1982, 1983, and 1984.

Biomass was estimated by volume displacement in 70% ethyl alcohol for major groups in all collections except those taken in 1972. Animals were blotted until no further wetting occurred and then transferred to a graduated cylinder. Appropriate conversion factors allowed expression of biomass in grams ash-free dry weight per square metre (Johnson 1970).

Results

Abundance of Major Taxa

Detailed examination of temporal trends within each of the major taxa was carried out by analysis of variance of data from both index and transect stations. Oligochaetes had significantly higher numbers at index stations in 1977 than in other years sampled (Fig. 2), while at transect stations during 1975, 1976, and 1977, numbers were significantly higher than in 1984 (Fig. 3). The Glenora and Conway index stations had significantly higher mean numbers than the Big Bay and Lake Ontario index stations. Analysis of variance confirmed peak abundance of oligochaetes in the mid-1970s and reduction in the 1980s. Trends in species composition of oligochaete associations, and other major taxa, will be examined later.

The rise and decline of sphaeriids also was substantiated statistically. Mean sphaeriid numbers at the index stations were higher in 1977 than in other years sampled, while numbers in 1976 were higher at the transect stations. Recent numbers of sphaeriids were lower than those observed in the earliest study; 1983 and 1984 means at index stations were significantly lower than 1967 and 1968 means. Also, 1984 numbers were lower than 1982 sphaeriid numbers. The Glenora index station represents the area of greatest abundance of sphaeriids. The upper bay, represented by the Big Bay station, continues to be extremely poor habitat for sphaeriids. Not a single specimen was recovered from 18 samples taken in 1982–84, compared with 14 specimens in 24 samples in August collections of earlier years.

Our analysis indicated significantly higher numbers of chironomids prior to the 1980s at index stations; the 1968 numbers were higher than all three years 1982–84, and the 1977 mean was greater than the 1982 mean. There were no significant differences among means for chironomids at transect stations.

The apparent downward trend in isopod (*Caecidotea racovitzai*) numbers was confirmed by analysis of variance. At index stations, mean numbers in 1982–84 were less than in 1967–68; the mean in 1972 also was lower than in 1967–68, and in 1977 it was lower than in 1968 but not 1967. At lower bay transect stations in some years of the mid-1970s (1974, 1976, 1977), mean isopod numbers were higher than in all years in the

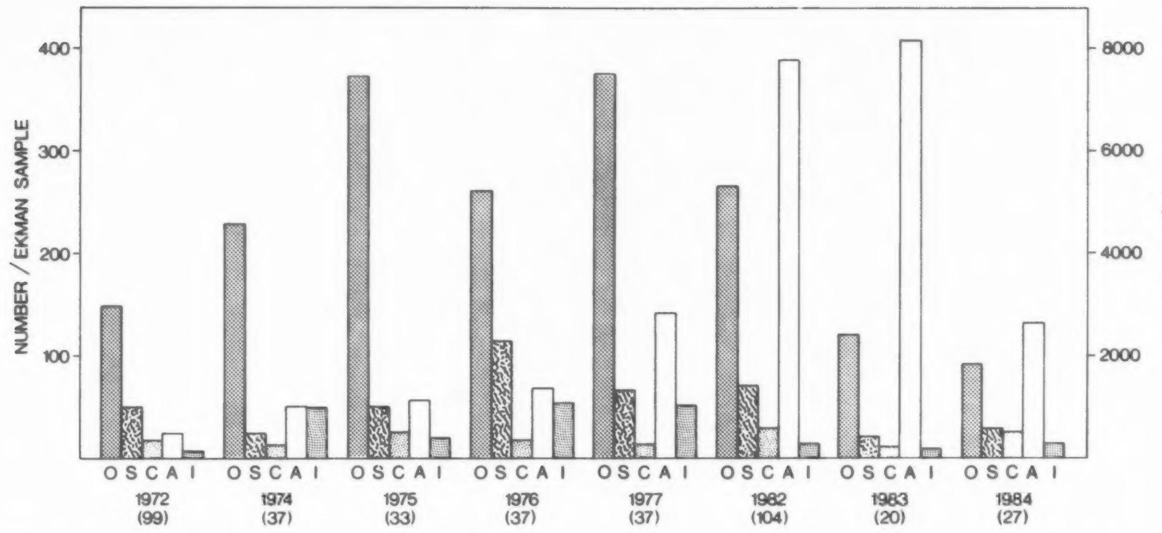

FIG. 3. Mean numbers of individuals of major macroinvertebrate groups collected at transect stations in the lower bay during 1972–84. The number of Ekman samples for each data set is shown in parentheses. Groups are as follows: O, oligochaetes; S, sphaeriids; C, chironomids; A, amphipods; I, isopods.

TABLE 1. Standing stocks of macroinvertebrates at the index stations (g ash free dry weight/m^2) sampled in August in six years (standard error in parentheses).

Year	Chironomids	Oligochaetes	Sphaeriids	Isopods	Amphipods	Total
Big Bay						
1967	0.60(0.084)	0.33(0.084)	< 0.01	—	—	0.93(0.11)
1968	0.68(0.040)	0.02(0.002)	< 0.01	—	0.02(0.020)	0.70(0.04)
1977	1.41(0.137)	0.36(0.030)	—	—	—	1.77(0.12)
1982	0.88(0.209)	0.48(0.090)	—	—	—	1.36(0.21)
1983	0.44(0.065)	0.68(0.107)	—	—	0.02(0.017)	1.14(0.12)
1984	0.12(0.026)	0.21(0.041)	—	—	0.03(0.027)	0.35(0.06)
Glenora						
1967	1.12(0.130)	2.32(0.477)	0.46(0.031)	5.97(1.518)	0.03(0.009)	9.90(1.59)
1968	1.58(0.174)	2.32(0.231)	0.62(0.047)	0.76(0.095)	0.02(0.005)	5.30(0.30)
1977	0.77(0.061)	2.34(0.511)	0.58(0.146)	0.09(0.040)	0.04(0.018)	3.82(0.68)
1982	0.58(0.109)	0.87(0.186)	0.09(0.026)	0.10(0.069)	0.08(0.33)	1.72(0.29)
1983	1.04(0.194)	0.20(0.060)	0.05(0.004)	0.05(0.004)	0.21(0.037)	1.55(0.25)
1984	0.82(0.126)	0.08(0.017)	0.03(0.006)	0.03(0.021)	0.10(0.010)	1.06(0.14)
Conway						
1967	0.24(0.039)	0.09(0.011)	0.15(0.008)	0.19(0.020)	6.35(0.281)	7.02(0.29)
1968	0.18(0.044)	0.27(0.054)	0.23(0.027)	0.29(0.051)	5.12(0.113)	6.09(0.14)
1977	0.02(0.009)	2.13(0.396)	0.35(0.070)	1.20(0.271)	0.05(0.034)	3.75(0.67)
1982	0.19(0.081)	0.53(0.093)	0.08(0.025)	0.19(0.063)	0.90(0.268)	1.89(0.46)
1983	0.11(0.021)	0.23(0.055)	0.05(0.016)	0.06(0.028)	2.08(0.352)	2.53(0.37)
1984	0.58(0.092)	0.36(0.062)	0.03(0.008)	0.02(0.017)	1.20(0.209)	2.19(0.30)
Lake Ontario						
1967	0.13(0.019)	0.14(0.027)	0.15(0.031)	0.15(0.031)	4.43(0.458)	5.00(0.46)
1968	0.04(0.024)	0.16(0.043)	0.24(0.045)	0.02(0.004)	4.81(1.124)	5.27(1.13)
1977	0.01(0.005)	0.72(0.069)	0.16(0.018)	0.11(0.034)	6.00(0.264)	7.00(0.31)
1982	0.04(0.012)	0.45(0.055)	0.32(0.037)	0.06(0.012)	2.60(0.250)	3.47(0.26)
1983	0.01(0.008)	0.28(0.060)	0.14(0.032)	0.26(0.052)	1.90(0.260)	2.59(0.30)
1984	0.01(0.007)	0.17(0.042)	0.04(0.003)	0.11(0.010)	1.38(0.147)	1.71(0.17)

1980s. In 1967–68, isopods were most abundant at the Glenora index station, but by 1977, numbers had become greater at the Conway station, and in 1983 and 1984, numbers were higher at the Lake Ontario index station than at Glenora and Conway. However, populations in the 1980s at all stations were extremely low compared with the 1967 and 1968 populations at Glenora.

The numbers of amphipods declined after 1968 but they recovered between 1977 and 1982. Mean numbers at index stations in 1967 and 1968 were significantly higher than in other years except 1983, and the 1984 mean was lower than the 1983

TABLE 2. Values of PSC (%) for each series of samples at index stations compared with all other series (methods are described in the text).

Year	1967	1968	1972	1977	1982	1983	1984
Big Bay							
1967	—						
1968	49–60	—					
1972	33–46	21–45	—				
1977	8–15	5–9	6–16	—			
1982	21–35	22–32	23–38	46–62	—		
1983	27–51	20–30	29–39	20–57	71–80	—	
1984	16–58	14–31	16–40	11–45	53–79	52–78	—
Glenora							
1967	—						
1968	63–77	—					
1972	47–56	42–51	—				
1977	19–51	18–42	22–46	—			
1982	13–23	17–22	15–19	24–64	—		
1983	26–42	33–48	24–37	15–30	47–59	—	
1984	2–47	14–28	12–17	2–7	24–41	57–67	—
Conway							
1967	—						
1968	75–82	—					
1972	6–26	14–32	—				
1977	4–8	9–14	48–63	—			
1982	78–89	72–82	9–30	10–16	—		
1983	88–90	66–75	1–22	1–4	74–86	—	
1984	62–81	68–93	13–28	9–16	68–90	59–80	—
Lake Ontario							
1967	—						
1968	77–89	—					
1972	64–75	60–78	—				
1977	64–71	65–71	64–74	—			
1982	73–83	69–80	57–71	63–74	—		
1983	72–83	65–78	55–66	62–73	70–76	—	
1984	74–84	65–87	59–64	59–69	69–71	80–90	—

mean. At the Glenora index station the amphipod population peaked in 1982 and 1983. Two peaks were observed at Conway, the first in 1967–68 and the second in 1983 of approximately the same magnitude. At the Lake Ontario station, peaks occurred in 1968 and 1977 with a slow decline thereafter. At the transect stations, which were selected to cover the area of greatest abundance of *P. hoyi*, the 1982 and 1983 means were higher than in all surveys throughout the 1970s, and although the population decreased in 1984, it remained significantly greater than in 1972, the year of their lowest numbers.

Standing stocks of macroinvertebrates declined through the period 1977–84 at all index stations and from 1967 at Glenora and Conway (Table 1). Standing stocks declined from 1977 to 1984 by 80% at Big Bay, 72% at Glenora, 42% at Conway, and 75% at the Lake Ontario index station. Comparison of mean phytoplankton volumes for 1972–77 and 1978–81 showed reduction by 50% at Big Bay, 24% at Glenora, and 60% at Conway (Nicholls et al. 1986).

Standing stocks of main taxa of benthic macroinvertebrates were closely correlated with numbers. Correlation coefficients of station-year means were 0.877 for chironomids, 0.823 for oligochaetes, 0.859 for sphaeriids, 0.702 for isopods, and 0.925 for amphipods (all highly significant, $P < 1\%$ and $N = 18–24$). Therefore, examination of standing stocks provided little additional information beyond the analysis of variance of numerical abundance of major taxa; however, these data are useful in interpretation of trends in production in fish, biomass of food organisms being more useful than numbers (Hurley 1986).

Changes in Species Composition at Index Stations

PSC analysis

Our statistical analysis of change in species composition is based on confidence intervals about values of PSC, by which each sample series was compared with sample series in other years within each index station (Table 2). The values of PSC along each diagonal are a series in which consecutive sampling times are compared. With gradual change the highest values would be expected along the diagonal, and the lowest values would be expected in the bottom left corner where PSC values are for most distant sampling times. The lowest of the values along the diagonal indicates the interval of greatest change in species composition. The bottom left value shows the degree of change from beginning to end of our data base.

Species composition of the macroinvertebrate community at the Big Bay index station changed most between 1972 and 1977, much more than between 1977 and 1982. As might be expected the 1967 and 1968 communities were similar and those sampled through the 1980s were similar. The overall change from 1967–68 to the 1980s was substantial (Table 2). The Glenora index station also showed considerable change from 1967 to 1984, with most change occurring between 1972 and 1977, closely followed by the change from 1977 to 1982. The macroinvertebrate community at Conway showed considerable change between 1977 and 1982, but the change during the 1968–72 interval was also large. In contrast with the Big Bay and Glenora stations, however, the change at Conway from beginning to end and specifically 1967–68 compared with

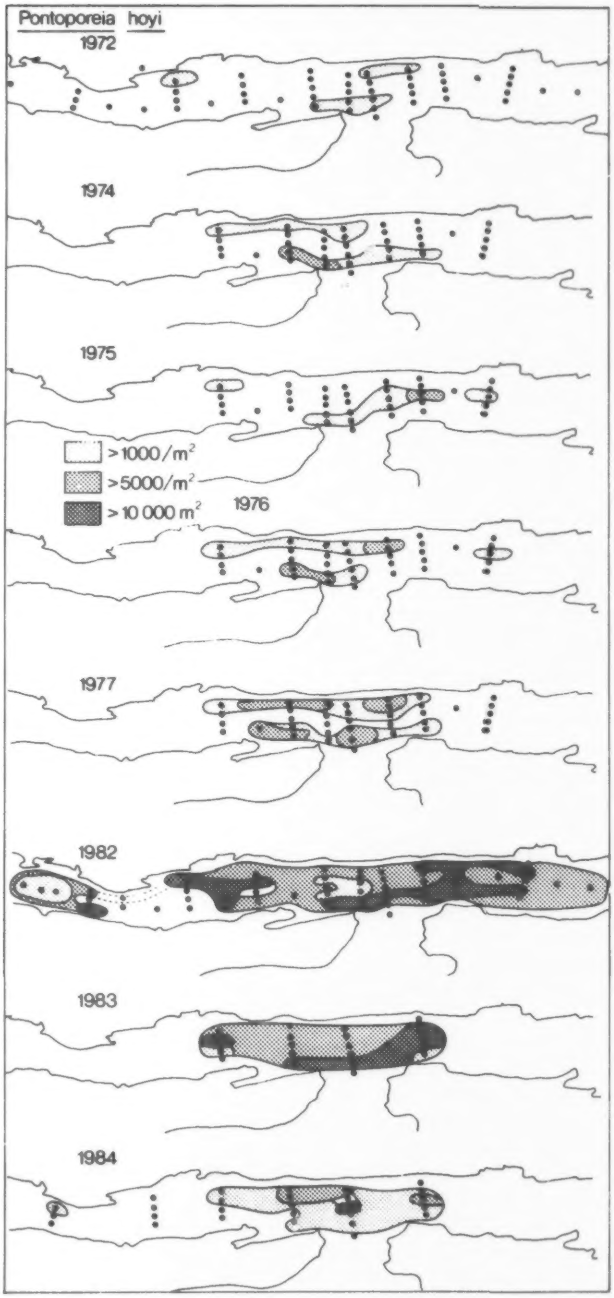

FIG. 4. Abundance of *Pontoporeia hoyi* in August transect station samples from the lower bay. A total of 52 stations were sampled in 1972 and 1982 whereas 20–37 stations were sampled for other years.

1982–84 was minimal. Therefore, while there were substantial shifts in species composition during the 1970s, by the 1980s the Conway community resembled that observed in the late 1960s. Greater stability at the Lake Ontario index station was clearly indicated by the set of close PSC values (Table 2), with lower confidence limits never less than 55%.

Therefore, analysis of PSC suggests that much more change in macroinvertebrate communities occurred within the Bay of Quinte than in outer Adolphus Reach and adjacent Lake Ontario. In the following paragraphs we shall describe the most significant shifts in species composition.

Species accounts

By 1984, species composition at Big Bay had shown a significant change from the earliest work done in the period 1967–68. Main shifts in species were as follows. The oligochaetes *Limnodrilus hoffmeisteri* and *Tubifex tubifex* increased in numbers from 1967 to 1977, while numbers of *Aulodrilus pigueti* declined and *Ilyodrilus templetoni* was absent in 1977 (and was not collected again until 1983). After 1977, *A. pigueti* was not collected and *T. tubifex* became scarce. *Aulodrilus pluriseta* and *Limnodrilus profundicola* were collected in 1977 only. *Quistadrilus multisetosus* was present only until 1982, and *Spirosperma ferox* appeared in low numbers in 1982–84. The chironomid *Harnischia amachaerus*, common in 1967–68, disappeared by 1972. Numbers of *Procladius* spp. dropped sharply from 1972 to 1977 and declined steadily thereafter. The large *Chironomus* spp. were relatively uniform in numbers through the period except *C. plumosus* which peaked in 1977.

Substantial changes in species composition also occurred at the Glenora station from beginning to end of the study period. The increase in oligochaetes in 1977, particularly *L. hoffmeisteri* and *T. tubifex*, and the disappearance of *Potamothrix bavaricus* contributed to the differences from earlier years. *Aulodrilus pluriseta* was common until it declined in 1984. By the 1980s, oligochaetes declined to low numbers of five species, while eight species of oligochaetes had been collected at their peak. Sphaeriid numbers also peaked in 1977, with eight species collected; by 1984 only *Pisidium casertanum* was collected in low numbers. Generally, numbers of chironomids have been relatively stable in the Glenora community, with three *Chironomus* spp. (*C. anthracinus*, *C. atritibia*, and *C. plumosus*) and *Procladius* spp. comprising almost all of the chironomid population each year. The population of the isopod *C. racovitzai* declined between 1968 and 1972 and remained at low numbers. The major change in the period 1982–84 was the increase in numbers of the amphipod *P. hoyi*. At Glenora, *P. hoyi* was scarce in 1967–68, but its numbers increased by more than one order of magnitude between 1977 and 1982–83, and then declined again in 1984 to about 25% of peak population size. This change will be described in greater detail subsequently using data from transect stations in Adolphus Reach.

At Conway the species composition at the end of the sampling period was similar to that at the beginning. This response was different than at Big Bay and Glenora where species composition continued to change throughout the sampling period. At Conway, species composition in the 1982–84 samples was very similar to that of the 1967 and 1968 samples, partly attributable to the decline in *P. hoyi* in the 1970s and recovery in the 1980s. Other common species included the tubificids *L. hoffmeisteri* and *T. tubifex*, the chironomids *Procladius* spp., *Tanytarsus* spp., and *Microspectra* nr. *dives*, and the sphaeriids *P. casertanum*, *P. conventus*, and *P. lilljeborgi*. Species composition in 1972 and 1977 was similar. While oligochaetes were lower in numbers in the 1980s than in 1967–68, there were only minor changes in species composition. In 1982–84, *Potamothrix vejdovskyi*, *P. moldaviensis*, *S. ferox*, and *I. templetoni* were collected again following their absence in the 1972 and 1977 samples. The chironomid *Tanytarsus* spp. was scarce at the beginning and end of the sampling period. Numbers of *Micropsectra* sp. increased in the 1980s, while *Tanytarsus* spp. numbers declined. *Procladius* spp. numbers were lowest in 1972 and 1977. The amphipod *P. hoyi* had been reduced to about 1% of its

TABLE 3. Mean numbers of *Pontoporeia hoyi*, *Gammarus fasciatus*, and *Caecidotea racovitzai* per square meter in transect surveys each August of eight years (standard errors in parentheses).

Year	Species	Depth (m)			
		<25	25–35	36–45	>45
1972	*P. hoyi*	580 (206)	720 (348)	340 (240)	80(62)
	G. fasciatus	68 (10)	38 (24)	14 (6)	46 (30)
	C. racovitzai	50 (24)	100 (16)	80 (24)	74 (16)
1974	*P. hoyi*	1100 (294)	1560 (848)	1760 (1742)	60 (34)
	G. fasciatus	26 (140)	26 (8)	0	2 (2)
	C. racovitzai	504 (200)	1926 (502)	864 (738)	752 (368)
1975	*P. hoyi*	440 (168)	1440 (1070)	2440 (2432)	500 (188)
	G. fasciatus	50 (18)	0	10 (6)	88 (62)
	C. racovitzai	622 (204)	188 (96)	244 (106)	250 (90)
1976	*P. hoyi*	1100 (362)	2660 (1530)	1420 (1026)	940 (582)
	G. fasciatus	120 (38)	194 (138)	14 (8)	70 (56)
	C. racovitzai	1498 (392)	2566 (1598)	466 (184)	626 (342)
1977	*P. hoyi*	2940 (744)	7880 (2748)	2100 (1614)	900 (682)
	G. fasciatus	14 (6)	44 (32)	20 (12)	10 (4)
	C. racovitzai	1096 (348)	2016 (770)	678 (380)	694 (194)
1982	*P. hoyi*	9600 (1188)	8960 (1240)	2960 (826)	8260 (1134)
	G. fasciatus	8 (2)	24 (10)	52 (14)	74 (46)
	C. racovitzai	90 (18)	220 (30)	700 (166)	358 (78)
1983	*P. hoyi*	6880 (1418)	13900 (920)	8120 (898)	8360 (3138)
	G. fasciatus	8 (8)	0	6 (6)	12 (8)
	C. racovitzai	30 (12)	760 (700)	340 (250)	336 (262)
1984	*P. hoyi*	3060 (696)	2140 (1020)	1400 (756)	3660 (2382)
	G. fasciatus	14 (10)	0	0	56 (12)
	C. racovitzai	22 (10)	632 (260)	106 (50)	896 (352)

former abundance by 1972 and 1977 at the Conway index station, and by 1983 it had regained its earlier population size. Therefore, the main change resulted from the inverse trends in *P. hoyi* abundance and that of oligochaetes, sphaeriids, and isopods.

Species composition at the Lake Ontario index station was relatively uniform throughout the period. Numbers of *P. hoyi* were relatively stable, while other species (e.g. the chironomids *Procladius* sp. *Tanytarsus* spp., and *Micropsectra* sp. and the sphaeriids *P. casertanum*, *P. conventus*, and *P. lilljeborgi*) did not vary widely in abundance. At the Lake Ontario station, as at other index stations, oligochaetes declined after 1977.

Evidence from index stations suggests that in 1982–84 the macroinvertebrate community near the mouth of the bay and adjacent lake was returning to an association more typical of the early years 1967–68. The macroinvertebrate community in the upper and middle bay became increasingly different through the study period. There were no pronounced trends in species diversity through time, although increased *P. hoyi* numbers at Conway, particularly in 1982 and 1983, reduced species diversity.

Changes in Species Composition at Transect Stations

The most significant change in benthic macroinvertebrate communities at the transect stations was probably the increase in numbers of *P. hoyi* in Adolphus Reach, documented here by transect station samples collected in 1972–84 (Fig. 4; Table 3). Changes in numbers in four depth zones, which could be important in sorting out responses to oxygen conditions and predation pressure by fish, showed that *P. hoyi* increased at all zones but the deepest zone by 1977. Peak numbers of *P. hoyi* were reached in 1982 in the shallowest zone, and in 1983 in the deeper zones (Table 3). *Pontoporeia hoyi* had maintained low populations at intermediate depths through the period 1972–77, and then expanded in abundance first in shallower and then in deeper sediments (Fig. 4). Numbers of *Gammarus fasciatus* remained low relative to *P. hoyi* even in 1982–84. The isopod *C. racovitzai* occurred in moderate numbers through the period 1974–82, and it decreased in 1983–84 (Fig. 3).

In addition to the significant shifts in crustacean species abundance, there were several obvious trends in oligochaetes shown by transect station data. The increases and declines in populations of the oligochaetes *L. hoffmeisteri*, *T. tubifex*, and *P. vejdovskyi* were all similar to changes in total oligochaetes described earlier, but four other species showed different trends. *Quistadrilus multisetosus* was abundant ($>1000/m^2$) in the mid-1970s, rare in 1982 and 1983, and not collected in 1984. In contrast, *S. ferox*, which had not been collected from 1974 to 1977, became common ($100–500/m^2$) in the 1980's. Most stations that had high *Q. multisetosus* numbers also had highest *S. ferox* numbers in the 1980s (up to about $3000/m^2$). *Stylodrilus heringianus* occurred at several stations in the 1980s. This species was common in adjacent Prince Edward Bay and Lake Ontario collections, but in the bay proper only a dozen specimens were collected in 1977 and none before that. Among the oligochaetes, *A. pluriseta* was unusual, with substantial numbers in 1975–77, whereas it was absent in samples before 1975 and again in 1984.

Few trends were apparent in relative abundance of chironomid species at transect stations. *Procladius* spp. numbers declined to lowest numbers from 1974 to 1977 and recovered in the 1980s, a trend also observed at the Conway index station. Abundance of the chironomids *C. anthracinus* and *C. plumosus*

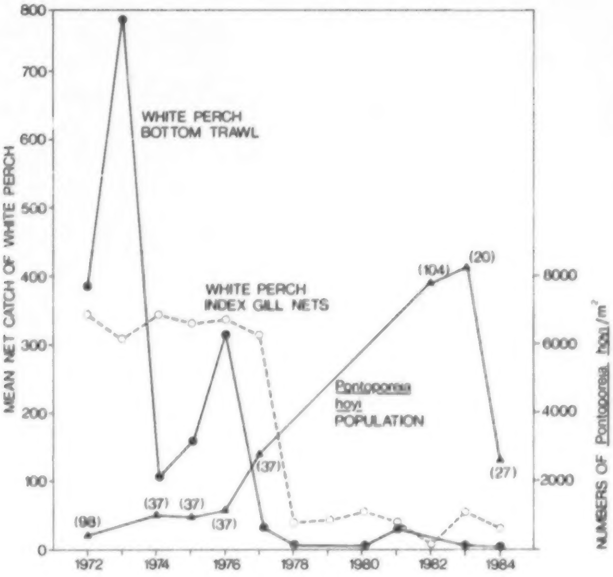

FIG. 5. Relationship between *Pontoporeia hoyi* mean numbers at transect stations and white perch bottom trawl and index gill net catches in the lower Bay of Quinte.

declined through the 1970s and both were rare in the 1980s. In contrast, *C. atritibia* increased in the 1980s. *Microspectra* sp. and *Tanytarsus* spp. showed considerable variability in numbers, which tended to be inversely related.

Sphaeriid numbers declined in transect samples in the 1980s, but not all of the major species declined. *Pisidium casertanum*, the commonest sphaeriid, and *P. ventricosum* declined, but numbers of *P. lilljeborgi* and *Sphaerium nitidum* apparently were maintained. Other common sphaeriids, for example, *Pisidium subtruncatum* and *P. henslowanum*, occurred in variable numbers with no obvious temporal trend.

Observations on Other Species

Greatest diversity in species was observed in the middle reaches of the bay (e.g. the Glenora index station). Here, the associations of the eutrophic inner bay mingle with species found in oligotrophic Lake Ontario and with additional species which are abundant only under apparently mesotrophic conditions (Johnson and Brinkhurst 1971a). The Lake Ontario macroinvertebrate community was less diverse than communities in the bay.

During the 1972–82 sampling, 97 taxa were identified from Ekman samples, compared with 128 taxa found in 1966–68. During the entire period, 28 taxa of oligochaetes, 25 sphaeriids, 49 chironomids, 6 crustaceans, 19 gastropods, and 28 miscellaneous taxa were identified. These are listed, with notes on temporal and spatial variations in three sampling periods, 1966–68, 1972–77, and 1982–84, in the Appendix.

Discussion

Fish–Macroinvertebrate Interactions

In 1972 it appeared that *P. hoyi* was poised for extinction in the Bay of Quinte, perhaps because of worsening oxygen conditions in the lower bay, especially in deeper waters. Now, strong evidence indicates that large populations of white perch (*Morone americana*) maintained very heavy predation pressure on *P. hoyi* (Hurley 1986), and with the collapse of the white perch in 1977, numbers of *P. hoyi* increased (Fig. 5), attaining a level more typical of populations at comparable depths in eastern Lake Ontario. For example, in Prince Edward Bay adjacent to the mouth of the Bay of Quinte, 3000–10 000 *P. hoyi*/m² were collected in each August through the sampling period.

Oxygen concentration data have been interpreted in detail by Minns and Johnson (1986). For the purpose of this study, oxygen levels only during late August 1 m above bottom sediments at transect stations were examined to assess whether conditions had improved during the sampling period. No significant differences were noted among mean oxygen concentrations in the five years 1974, 1975, 1976, 1977, and 1982 during the last 10 d of August. Lower minima than those observed in 1974–82 were noted in occasional sampling during the period 1967–72. However, Minns and Johnson (1986) concluded that there was no obvious difference in oxygen concentrations in the lower bay hypolimnion between years before and after phosphorus reductions at wastewater treatment plants. Oxygen depletion in the lower bay might have affected the vertical and east–west distribution of *P. hoyi*. However, because *P. hoyi* numbers declined even in areas of highest environmental suitability, apparently independently of oxygen conditions, the hypothesis of suppression of *P. hoyi* by a large population of stunted white perch appears likely.

White perch fed heavily on *P. hoyi* (Hurley 1986). In fact, this population of white perch congregating in the lower bay did not feed on fish at any size, probably because of their slow growth rates and small size at high population levels (Minns and Hurley 1986). White perch appeared to be widely distributed by depth (D. A. Hurley, pers. comm.). Although *G. fasciatus* occurred in much lower numbers in our samples than *P. hoyi*, it was preferred by the other major feeders on invertebrates, that is, by the rainbow smelt (*Osmerus mordax*) and yellow perch (*Perca flavescens*). The diet of trout-perch (*Percopsis omiscomaycus*) was similar to that of white perch but its numbers were considerably less in the 1970s (Hurley 1986). However, trout-perch, rainbow smelt, and common white sucker (*Catostomus commersoni*) have increased since the decline of white perch (D. A. Hurley, pers. comm.). The decline in *P. hoyi* in 1984 might be the result of increased predation by these species.

In summary, *P. hoyi* probably always has been confined within the bay to the cooler water of the lower bay, benefiting from the intrusion of Lake Ontario water. Maximum numbers of *P. hoyi* are found at intermediate depths in large, deep lake basins, as shown in Lake Superior (Freitag et al. 1976), Lake Huron (Schuytema and Powers 1966), Lake Michigan (Mozley and Alley 1973), and the Straits of Mackinac (Henson 1970). Generally, at these depths, the oxygen concentrations are high, temperatures cool, and the sediments are composed of fine sand and silt. Probably *P. hoyi* does not inhabit the middle bay above Glenora because of higher summer temperatures and seasonal short-term oxygen depletion. Our data indicated that *P. hoyi* may have had greater recruitment at intermediate depths during the 1970s. Lower oxygen in the deepest zone of Adolphus Reach, compared with shallower zones, may have been responsible for lower numbers in deep water. A greater proportion of *P. hoyi* was found in the deepest zone in the 1980s compared with the 1970s (Table 3). While we have not been able to define any improvement in oxygen conditions, we cannot dismiss the possibility because productivity of the system declined after reductions in phosphorus input. Therefore, heavy predation pressure by white perch until 1977 through all depths and possibly suboptimal oxygen concentrations in the deepest areas restricted *P. hoyi* to low numbers at intermediate depths, the most favourable habitat for the species. After the dramatic decline of the white perch, *P. hoyi* increased in numbers (Fig. 4) and spread to other depths and up the bay toward Glenora.

Yellow perch, in contrast with white perch, expanded in population size during the period 1977–81 (Hurley 1986). Yellow perch consumed approximately 10 times more *G. fasciatus* than *P. hoyi*, presumably because yellow perch inhabits shallower zones. Our sampling did not extend inshore shallower than approximately 15 m; based on other observations on *G. fasciatus*, we have assumed that it was more abundant inshore than *P. hoyi*. Barton and Hynes (1976) found high numbers (up to 10000/m^2) in the littoral zone of the Great Lakes often in association with the alga *Cladophora* sp. Because our samples should reflect the relative temporal abundance of *G. fasciatus*, we suspect that the expansion of yellow perch numbers reduced abundance of *G. fasciatus*. Although *P. hoyi* and the isopod *C. racovitzai* were distributed similarly with depth, our data indicated that *C. racovitzai* declined after 1977 while the population of *P. hoyi* was recovering. Therefore, *C. racovitzai* numbers did not increase in relation to the collapse of the white perch population. Its decline might be related to the increase in other fish species and/or to the decline in productivity in the bay.

Species Trends and Water Quality

Several significant changes in species composition, particularly in oligochaete and chironomid communities, indicated that species which are known to decline as water quality deteriorates are species which increase when water quality is improved and the more tolerant species are reduced. Specifically, sharp declines throughout the bay after 1977 in the oligochaetes *L. hoffmeisteri*, *T. tubifex*, and *Q. multisetosus*, considered to be pollution-tolerant species (Cook and Johnson 1974), and the increase in the clean-water species *S. heringianus* at the bay mouth provide evidence of improved water quality. The peaks in abundance of *P. vejdovskyi* and *A. pluriseta* in 1977 transect samples, just before major reduction in phosphorus loadings, and their decline through the early 1980s indirectly support the interpretation of Brinkhurst et al. (1968) that *Potamothrix* spp. and *Aulodrilus* spp. increase with advancing eutrophication. Also, at Big Bay, *A. pigueti* was not collected after 1977. At Glenora, *A. pluriseta* declined in 1984. However, conflicting evidence was provided by the collection of *P. moldaviensis* at Conway in 1982–84 following its absence in the 1972 and 1977 samples.

Oligochaete associations of the Bay of Quinte throughout the sampling period fall between those characteristic of the extremes of advanced hypereutrophic and oligotrophic states. The bay did not have extremely high numbers of *L. hoffmeisteri*, *L. cervix*, *L. claparedeanus*, and *T. tubifex*, like those found in Hamilton Bay in the 1960s (Johnson and Matheson 1968), which characterize hypereutrophy more than moderate numbers of eurytopic *L. hoffmeisteri* and *T. tubifex*. Nor did the bay, even at its deepest point (55 m) near its mouth, have *Rhyacodrilus* spp., *Spirosperma nikolskyi*, or *Tubifex kessleri*, the oligochaete species typical of most oligotrophic conditions in the Great Lakes including the main basin of Lake Ontario (Hiltunen 1969).

Although numbers of most chironomid species (mainly subfamily Chironomini) were relatively stable, there were some significant species changes, particularly the decline in *C. anthracinus* and *C. plumosus* and the increase in *C. atritibia*. The latter species was considered less tolerant of enrichment than the former two, based on distributions in the bay (Johnson 1970). Causes are not apparent for some other changes in chironomid associations, for example, the disappearance of *H. amachaerus* at the Big Bay index station and fluctuations in numbers of *Tanytarsus* spp. and *Microspectra* sp. in the bay and adjacent Lake Ontario. Bay of Quinte collections of *Tanytarsus* were clearly of several species, some of which inhabited different parts of the bay. Therefore, interpretation of the presence of the genus *Tanytarsus* to indicate oligotrophic conditions (Brinkhurst et al. 1968) is not valid, although some species of *Tanytarsus* and the *Micropsectra* sp. (nr. *dives*) likely are intolerant to eutrophic conditions. The decline in *Procladius* spp. coincident with the increase in oligochaete numbers was unexpected because these predaceous chironomids are known to utilize oligochaetes, and some species of *Procladius* are tolerant of highly eutrophic conditions (Carr and Hiltunen 1965).

Sphaeriids decreased in numbers and species in index and transect samples. Insufficient understanding of ecological requirements and considerable variability in numbers of the main species make interpretation of trends by species difficult. However, most species apparently were reduced in numbers as productivity of the bay declined.

Reduction in Benthic Macroinvertebrate Production

The statistically significant decreases in the 1980s of total numbers of oligochaetes, sphaeriids, chironomids, and some formerly abundant members of other taxa such as *C. racovitzai* indicate declining production by the benthic macroinvertebrate community following reductions in phosphorus loadings and decline in primary production. The amphipod *P. hoyi* increased while many other species were decreasing, but in 1984 its population declined to about 25% of the 1982–83 population level. These reductions in standing stocks (Table 1) suggest a considerable decline in productivity at the benthic macroinvertebrate level.

The only data on production of macroinvertebrates were from 1967–68, but standing stocks were shown to be indicative of rate of production because turnover rate ($P:B$) was established by temperature (Johnson and Brinkhurst 1971b). Standing stocks of macroinvertebrates in the 1980s were considerably less than those prior to full implementation of the phosphorus reduction program. Therefore, production of macroinvertebrates probably declined through the extended period of phosphorus reductions and decline in primary production in the bay and Lake Ontario. However, with the large shifts in fish communities and potential for drastically altered predation pressure on macroinvertebrates, which is known to influence net production (Ball and Hayne 1952), we cannot assume that these standing stock reductions indicate a directly proportional change in production of macroinvertebrates. As well, the ecological implications of any reduction in production of macroinvertebrates, to fish in particular, may be partly offset by qualitative changes in the benthic macroinvertebrate community.

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References

Ball, R. C., and D. W. Hayne. 1952. Effects of the removal of a fish population on the fish food organisms of a lake. Ecology 33(1): 41–48.

Barton, D. R., and H. B. N. Hynes. 1976. The distribution of amphipoda and isopoda on the exposed shores of the Great Lakes. J. Great Lakes Res. 2(2): 207–214.

Brinkhurst, R. O., A. L. Hamilton, and H. B. Herrington. 1968. Components of the bottom fauna of the Great Lakes. Publ. 33, Great Lakes Institute, University of Toronto, Toronto, Ont. 44 p.

Carr, J. F., and J. K. Hiltunen. 1965.. Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnol. Oceanogr. 10(4): 551–569.

Cook, D. G., and M. G. Johnson. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 763–782.

Freitag, R., P. Fund, J. S. Mothersill, and G. K. Prouty. 1976. Distribution of benthic macroinvertebrates in Canadian waters of northern Lake Superior. J. Great Lakes Res., Int. Assoc. Great Lakes Res. 2(1): 177–192.

Henson, E. B. 1970. *Pontoporeia affinis* (Crustacia, Amphipoda) in the straits of Mackinac region. Proc. 13th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. 601–610.

Hiltunen, J. K. 1969. The benthic macrofauna of Lake Ontario. Tech. Rep. Great Lakes Fish. Comm. 14: 39–50.

Hurley, D. A. 1986. Effect of nutrient reduction on the diets of four fish species in the Bay of Quinte, Lake Ontario, p. 237–246. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G. 1970. Production, energy flow and structure in some benthic macroinvertebrate associations of Lake Ontario. Ph.D. thesis, University of Toronto, Toronto, Ont. 182 p.

1986. Phosphorus loadings and environmental quality in the Bay of Quinte, Lake Ontario, p. 247–258. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G., and R. O. Brinkhurst. 1971a. Associations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1683–1697.

1971b. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1699–1714.

Johnson, M. G., and D. A. Hurley. 1986. Overview of Project Quinte — 1972–82, p. 1–6. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G., and D. H. Matheson. 1968. Macroinvertebrate communities of the sediments of Hamilton Bay and adjacent Lake Ontario. Limnol. Oceanogr. 13(1): 99–111.

Johnson, M. G., and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43(5): 836–853.

Minns, C. K., and D. A. Hurley. 1986. Population dynamics and production of white perch, *Morone americana*, in the Bay of Quinte, Lake Ontario, p. 215–223. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., and M. G. Johnson. 1986. Temperature and oxygen conditions and oxygen depletion in the Bay of Quinte, Lake Ontario, p. 40–49. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Mozley, S. C., and W. P. Alley. 1973. Distribution of benthic invertebrates in the south end of Lake Michigan. Proc. 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. 87–96.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Sanders, H. L. 1960. Benthic studies in Buzzards Bay III. The structure of the soft-bottom community. Limnol. Oceanogr. 2: 138–153.

Schuytema, G. S., and R. E. Powers. 1966. The distribution of benthic fauna in Lake Huron. Publ. Great Lakes Res. Div., Univ. Mich. 155–163.

Appendix: Macroinvertebrate Communities

Table A.1. Annotated list of macroinvertebrates collected in the Bay of Quinte and adjacent Lake Ontario during the period 1966–84. Location abbreviations: LB, lower bay; MB, middle bay; UB, upper bay; BB, Big Bay index station; GL, Glenora index station; LO, Lake Ontario index station; W, widespread. Numerical abundance categories: abundant ($>1000/m^2$), very common ($500-999/m^2$), common ($100-499/m^2$), scarce ($<100/m^2$), and rare (occurring at one or two stations only at $<100/m^2$). Three time periods: prior to phosphorus removal (1966–68), following phosphorus reduction in detergents (1972–77), and after phosphorus reduction at waste-treatment plants (1982–84).

	1966–68	1972–77	1982–84
Oligochaeta			
Lumbriculidae			
Stylodrilus heringianus Claparede	LO: common	LB: rare	LB: common
Naididae			
Arcteonais lomondi (Martin)	—	LB: common	—
Chaetogaster diaphanus (Gruithuisen)	—	LB: rare	—
Nais pseudobtusa Piguet	—	LB: rare	—
N. variabilis Piguet	—	LB: rare	—
Nais sp.	LO: rare	LB: rare	—
Ophidonais serpentina (Muller)	—	LB: rare	—
Slavina appendiculata (d'Udekem)	—	LB: rare	
Stylaria lacustris (Linnaeus)	LB: rare	—	—
Tubificidae			
Aulodrilus limnobius Bretscher	LO: rare	LB: rare	—
A. pigueti Kowalewski	BB: v. common	BB + LB: common	—
A. pluriseta (Piguet)	LB + LO: v. common	BB + LB: common	GL: scarce
Ilyodrilus templetoni (Southern)	UB + LO: scarce	LB: rare	LB: rare
Isochaetides freyi (Brinkhurst)	LO: rare	—	—
Limnodrilus cervix Brinkhurst	UB: rare	—	—
L. claparedeanus Ratzel	LB: rare	LB: rare	LB: rare

APPENDIX. (*Continued*)

	1966–68	1972–77	1982–84
L. hoffmeisteri Claparede	W: abundant	W: abundant	W: v. common
L. profundicola (Verrill)	—	BB: rare	BB: rare
L. udekemianus Claparede	LO: rare	LB: rare	—
Potamothrix bavaricus (Oschmann)	GL: abundant	LB: rare	—
P. bedoti (Piguet)	LO: scarce	LB: rare	—
P. moldaviensis Vejdovsky & Mrazek	LB + LO: common	LB: rare	LB: rare
P. vejdovskyi (Hrabe)	LB + LO: common	LB: v. common	LB: common
Quistadrilus multisetosus (Smith)	UB + MB: scarce	LB + LO: abundant	LB + LO: rare
Spirosperma ferox (Eisen)	LO: common	LB: rare	LB: v. common
Tubifex tubifex (Muller)	W: common	W: abundant	W: common
Hirudinoidea			
Glossiphonidae			
Glossiphonia complanata (Linnaeus)	LO: rare	—	—
G. heteroclita (Linnaeus)	LO: rare	—	—
Helobdella stagnalis (Linnaeus)	W: scarce	LB: rare	LB: rare
Turbellaria			
Planariidae			
Phagocata spp.	LO: rare	—	—
Rhabdocoela			
Hydrolimax cf. *grisea* Haldeman	W: common	—	—
Gastropoda			
Sphaeriidae			
Pisidium adamsi Prime	LO: rare	—	—
P. amnicum (Muller)	LB: rare	LB: rare	—
P. casertanum (Poli)	W: common	LB + LO: v. common	LB + LO: common
P. compressum Prime	W: scarce	LB + LO: scarce	LB + LO: scarce
P. conventus Clessin	LO: abundant	LB + LO: common	LB + LO: scarce
P. equilaterale Prime	—	LB: rare	—
P. ferrugineum Prime	LO: rare	LB: rare	LB: rare
P. henslowanum (Sheppard)	W: common	LB + LO: scarce	LB + LO: scarce
P. idahoense Roper	LB + LO: scarce	LB + LO: scarce	LB: rare
P. lilljeborgi Clessin	W: common	LB + LO: common	LB + LO: scarce
P. nitidum Jenyns	LO: common	LB + LO: common	LB: scarce
P. n.f. pauperculum Jenyns	—	LB: rare	—
P. punctatum Sterki	LB: rare	LB: rare	LB: rare
P. subtruncatum Malm	W: scarce	LB: common	LB: common
P. variable Prime	LB: rare	LB: rare	LB: rare
P. ventricosum Prime	LB + LO: common	LB + LO: common	LB: scarce
P. walkeri Sterki	LB + LO: rare	—	—
Sphaerium corneum (Linnaeus)	LB + LO: common	LB + LO: scarce	—
S. lacustre (Muller)	MB + LO: rare	—	—
S. nitidum Clessin	LO: common	LB + LO: scarce	LB + LO: common
S. partumeium Say	GL: rare	LB: rare	—
S. securis (Prime)	—	LB: rare	—
S. simile (Say)	LB: rare	—	—
S. striatinum (Lamarck)	LB + LO: rare	LB: rare	LB + LO: rare
S. transversum (Say)	LO: rare	—	—
Unionidae			
Anodonta grandis grandis Say	W: common	—	—
Elliptio complanata (Lightfoot)	W: common	—	—
Lampsilis radiata radiata (Gmelin)	W: common	LB: rare	—
L. r. siliquoidea (Barnes)	W: common	—	—
Leptodea fragilis (Rafinesque)	BB: rare	—	—
Proptera alata (Say)	BB: rare	—	—
Bithyniidae			
Bithynia tentaculata (Linnaeus)	W: scarce	LB: scarce	LB: rare
Hydrobiidae			
Amnicola limosa (Say)	LO: common	LB: scarce	LB: rare
Probythinella lacustris (Baker)	UB + MB: rare	—	—
Lymnaeidae			
Fossaria obrussa Say	LO: rare	LB: rare	—
Lymnaea stagnalis jugularis (Say)	—	LB: rare	—
Pseudosuccinea columella (Say)	—	LB: rare	—
Stagnicola catascopium catascopium (Say)	—	LB: rare	—

APPENDIX. (*Continued*)

	1966–68	1972–77	1982–84
Physidae			
Physella gyrina gyrina Say	LO: rare	LB: rare	—
Planorbidae			
Gyraulus deflectus (Say)	LO: rare	—	—
G. parvus (Say)	LO: rare	LB: rare	—
Helisoma anceps anceps (Menke)	LB + LO: rare	—	—
Promenetus exacuous (Say)	LO: rare	—	—
Pleuroceridae			
Goniobasis livescens (Menke)	LO: rare	—	—
Valvatidae			
Valvata piscinalis (Muller)	MB + LB: rare	LB: rare	—
V. sincera sincera Say	LO: common	LB: scarce	W: scarce
V. tricarinata Say	W: common	LB: scarce	LB: rare
Viviparidae			
Viviparus georgianus (Lea)	—	LB: rare	—
Crustacea			
Asellidae			
Caecidotea racovitzai racovitzai (Williams)	LB + LO: abundant	LB + LO: common	LB + LO: common
Lirceus lineatus (Say)	LB + LO: common	LB: rare	—
Mysidae			
Mysis relicta (Loven)	LO: rare	—	LB: rare
Gammaridae			
Gammarus fasciatus Say	W: common	W: scarce	LB + LO: scarce
Hyalellidae			
Hyalella azteca (Saussure)	W: common	—	—
Pontoporeiidae			
Pontoporeia hoyi Smith	LB + LO: abundant	LB + LO: abundant	LB + LO: abundant
Insecta/Diptera			
Chironomini			
Chironomus anthracinus group[a]	W: v. common	BB + LB: common	LB: common
C. atritibia (Malloch)	LB + LO: common	LB: common	LB: common
C. plumosus (Linnaeus)	W: common	BB + LB: scarce	BB + LB. scarce
C. semi-reductus group[b]	UB + MB: scarce	LB: rare	LB: rare
Cladopelma sp.[c]	UB + MB: common	LB: rare	BB + GL: rare
Cryptochironomus digitatus (Malloch)[c]	W. common	BB + LB: scarce	BB + LB: rare
Dicrotendipes modestus (Say)[c]	W: common	BB + LB: rare	LB: rare
Einfeldia sp.	—	LB: rare	—
Endochironomus subtendens (Townes)[c]	UB + LO: common	—	—
Glyptotendipes sp.[d]	UB: rare	—	—
Harnischia sp.	BB: common; GL: rare	LB: rare	—
Microtendipes pedellus (DeGeer)	MB + LO: scarce	BB + LB: rare	LB: rare
Parachironomus abortivus (Malloch)[c]	LO: scarce	LB: rare	—
Paracladopelma sp.	LO: rare	BB: rare	—
Paralauterborniella sp.	—	LB; rare	—
Paratendipes albimanus (Meigen)	UB: scarce	LB: rare	LB: rare
Phaenopsectra spp.[e]	UB: rare	LB: rare	LB: rare
Polypedilum spp.[f]	W: scarce	BB:LB: rare	LB: rare
Pseudochironomus sp.	MB: rare	—	LB: rare
Stictochironomus sp.	MB: rare	GL: rare	—
Tanytarsini			
Cladotanytarsus sp.	LO: rare	—	—
Micropsectra nr. dives (Johannsen)	LB + LO: common	LB + LO: common	LB + LO: scarce
Paratanytarsus sp.	LO: rare	—	—
Tanytarsus sp.[g]	W: common	BB + LB: common	LB: scarce
Orthocladiinae			
Cricotopus sp.	LO: rare	—	—
Diplocladius sp.	BB: rare	—	—
Heterotrissocladius sp.	—	LO: rare	LB: rare

Appendix. (*Concluded*)

	1966–68	1972–77	1982–84
Hydrobaenus sp.	GL: rare	—	—
Parametriocnemus sp.	—	LB: rare	—
Psectrocladius spp.[h]	LO: rare	—	—
Tanypodinae			
Ablabesmyia americana Fittkau	LO: scarce	LB: rare	LB: rare
Clinotanypus cf. pinguis (Loew)	LB + LO: rare	—	—
Coelotanypus sp.	UB: common	BB: scarce	BB: scarce
Pentaneura sp.	LO: rare	—	—
Procladius spp.[i]	W: abundant	W: v. common	W: common
Psectrotanypus sp.	—	BB: rare	—
Ceratopogonidae			
Palpomyia sp.	W: scarce	—	—
Chaoboridae			
Chaoborus albatus Johnson	UB: scarce	BB: scarce	BB + GL: rare
Insecta/Trichoptera			
Leptoceridae			
Ceraclea diluta (Hagen)	LO: rare	—	—
Leptocerus americanus (Banks)	UB: rare	—	—
Mystacides sepulchralis (Walker)	MB + LB: rare	—	—
Nectopsyche albida (Walker)	LO: rare	—	—
Oecetis spp.[j]	LO: rare	—	LB: rare
Triaenodes sp.	LO: rare	—	—
Lepidostomatidae			
Lepidostoma sp.	LO: rare	—	—
Polycentropidae			
Phylocentropus sp.	LO: rare	—	—
Polycentropus sp.	UB: rare	—	—
Arachnida			
Arrenuridae			
Arrenurus sp.	MB: rare	—	—
Hygrobatidae			
Hygrobates sp.	LB: rare	—	—
Lebertiidae			
Lebertia sp.	MB: rare	—	—
Limnesiidae			
Limnesia sp.	UB + MB: scarce	—	—
Pionidae			
Piona sp.	W: scarce	—	—
Unionicolidae			
Neumania sp.	UB + MB: scarce	—	—
Unionicola sp.	W: scarce	—	—

[a] Includes *C. attenuatus* Walker and *C. anthracinus* (Zetterstedt) (Johnson and Brinkhurst 1971a, appendix I).

[b] Includes *C.* sp. A and *C.* sp. B (Johnson and Brinkhurst 1971a, appendix I).

[c] Genus previously given as *Chironomus* (Johnson and Brinkhurst 1971a, appendix I).

[d] Includes *G.* sp. A and *G.* sp. B (Johnson and Brinkhurst 1971a, appendix I).

[e] Includes *Tribelos jucundus* (Walker).

[f] Includes *P. cf. nebeculosum* (Meigen) and *P. cf. simulans* Townes (Johnson and Brinkhurst 1971a, appendix I).

[g] Includes at least four species (Johnson and Brinkhurst 1971a, appendix I).

[h] Includes *P.* sp. A *P.* sp. B and *P.* sp. C (Johnson and Brinkhurst 1971a, appendix I).

[i] Includes *P. bellus* (Loew), *P. denticulatus* Sublette, *P. freemani* Sublette, and *P. sublettei* Roback.

[j] Includes *O.* sp. A (Johnson and Brinkhurst 1971a, appendix I).

Shoreline Fauna of the Bay of Quinte

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comparison of overlay maps of the Bay of Quinte dating from 1929 showed that some marshes have been drained, and in some areas the shoreline has moved inland slightly. The fauna has not been sampled regularly or systematically, and therefore, information on aquatic macroinvertebrates, reptiles, amphibia, birds, and mammals was sought from accounts in the literature supplemented by personal communications from practising biologists. Populations of breeding ducks have declined, while the proportion of mallards has increased. Migratory wildfowl are less abundant than might be expected in the habitat. Numbers of visiting birds, such as herring gulls, reflect breeding success on offshore islands. Trapping records show a variable low density of muskrats.

Une comparaison de cartes superposées de la baie de Quinte établies depuis 1929 a révélé que certains marécages ont été asséchés et qu'à certains endroits, le littoral s'est légèrement déplacé vers l'intérieur des terres. La faune n'a pas été échantillonnée régulièrement ou systématiquement : les données sur les macroinvertébrés, reptiles, amphibiens, oiseaux et mammifères aquatiques ont donc été obtenues de comptes rendus publiés en plus de communications personnelles auprès de biologistes actifs. Les populations de canards reproducteurs ont diminué tandis que le nombre de mallards a augmenté et les oiseaux aquatiques migrateurs sont moins abondants que prévu dans un tel habitat. Le nombre d'oiseaux visiteurs, comme le goéland argenté, traduit la réussite de la reproduction dans les îles au large du littoral. Les données de piégage révèlent une faible densité variable du rat musqué.

Introduction

This paper summarizes available information on the fauna of the Bay of Quinte and its shoreline during the past 50 yr. Its purposes are to provide an introduction to the natural history of the Bay of Quinte watershed, with emphasis on aquatic mammals and terrestrial and shoreline biota, and to identify any trends related to eutrophication.

Habitats

The shoreline consists of limestone cliffs, shingle or sand beaches, and marshes. Most of the records discussed in this paper are from the marshes.

Changes in wetland vegetation have been discussed in Crowder and Bristow (1986). There has been a loss of species richness which is now particularly low in the Belleville–Big Bay marshes. Larger beds of wild rice formerly existed, and there is some evidence that wild celery and sago pondweed, all important as food for birds, have diminished in area. Areas of cattails appear to have increased.

Diminution of wetlands during the historical period has been estimated by Whillans (1982) to be 6.2% for shoreline marshes in Prince Edward County and 3.6% for inland marshes. A higher loss would be expected in shoreline marshes on the north side of the Bay of Quinte because of its more dense urban population.

Areas of wetland within the Bay of Quinte were compared by using overlays from topographical maps based on surveys flown in 1929, 1948, 1976, and 1979. In 1929 and 1948 the mean annual water level was higher than in 1979 (Sly 1986), which should have caused the shoreline to be further inland in the earlier period unless local changes occurred. The cultural change to a drier marsh, described by Whillans (1982), occurred in an area of about 200 ha on the south shore in the Deseronto area; paradoxically, there are fewer tracks and houses now in this area than in 1929. In the same region, a marsh at Unger Island has been drained. In the Trenton region, near Dead Creek and Carrying Place, an area of about 50 ha has been drained since 1929, while approximately 3 km of fringing marsh east of Trenton has been developed.

In the Huff Island region, although the edge of the marsh has moved slightly inland since 1929, changes are negligible in relation to the large wetlands.

Hay Bay, with large cattail marshes which can become floating islands, has changed considerably. The shoreline has moved inland since 1948 except immediately east of the mouth of Wilton Creek. The area of emergent wetland in 1979 was about 250 ha less than in 1948.

TABLE 1. Macroinvertebrate larvae, etc., associated with macrophytes in the Bay of Quinte. Data represent no. · g dry wt $^{-1}$ (no. · m plant $^{-2}$). From N. Gerrish and J. M. Bristow (unpubl. data). E = *Elodea canadensis*, M = *Myriophyllum spicatum*, V = *Vallisneria americana*, C = Ceratophyllum demersum.

	Adolphus Reach								Belleville							
	June, water temp. 15°C				July, water temp. 19°C				June, water temp. 22°C				July, water temp. 22°C			
Taxon	E	M	V	C	E	M	V	C	E	M	V	C	E	M	V	C
Hydrobiidae	51 (147)	199 (334)	635 (4636)	71 (399)	138 (429)	826 (1388)	162 (1183)	132 (797)	—	0.4 (4)	4 (15)	1 (2)	18 (22)	<0.1 (1)	3 (11)	14 (23)
Valvatidae	—	11 (19)	85 (621)	8 (48)	—	—	—	—	—	—	—	5 (8)	3 (4)	—	15 (56)	1 (2)
Physidae	—	49 (82)	215 (1570)	7 (42)	22 (64)	523 (879)	18 (131)	33 (199)	—	—	—	—	7 (9)	0.2 (2)	—	2 (3)
Planorbidae	5 (15)	22 (37)	—	2 (12)	6 (17)	181 (304)	2 (15)	3 (18)	30 (37)	—	—	—	—	2 (20)	10 (37)	34 (57)
Lymnaeidae	0.8 (2)	—	—	—	—	3 (5)	—	—	—	—	—	—	—	—	—	—
Sphaeridae	—	—	20 (146)	—	—	3 (5)	—	—	10 (15)	—	—	—	—	—	—	—
Chironomidae	10 (29)	5 (8)	150 (1095)	21 (127)	—	8 (13)	5 (37)	1 (6)	68 (84)	67 (680)	—	15 (25)	2 (3)	39 (396)	36 (134)	2 (3)
Lepidoptera	0.7 (2)	—	—	2 (12)	—	—	—	0.2 (1)	—	0.8 (8)	—	—	—	—	—	—
Odonata	—	—	—	0.2 (1)	—	—	—	—	1 (1)	—	—	—	—	—	—	—

Although the Unger Island area has become less diversified, Hay Bay retains a mixture of pools and emergent vegetation that should still be good habitat for wildfowl. Parts of both the north and south shores were more indented in 1979 than in 1948.

In 1979, the area of wetland was conservatively estimated at 4074 ha, and in 1929 it was 8–10% larger despite higher water levels.

As part of a comparative ranking of 35 southern Ontario wetlands, three shoreline marshes in the Bay of Quinte were evaluated by the Canadian Wildlife Service in 1983 (Maltby et al. 1983). The survey was done in the summer and did not include a component on migratory birds. Overall scoring, which was partly based on recreational values and amenities, ranked Hay Bay as a wetland of high significance and Big Island Marsh and Muskote Bay as moderately significant. Some biological components of the scores were as follows:

	Hay Bay	Big Island	Muskote Bay
Productivity (maximum 80)	64	64	63
Diversity (maximum 120)	94	95	84
Rarity (maximum 250)	180	230	130
Significant habitat (maximum 250)	45	80	70

In comparison with other wetlands of Prince Edward County, such as Presqu'ile Bay, East Bay, and Big Swamp, Big Island Marsh and Hay Bay were ranked first and third and Muscote Bay seventh out of a total of 15.

Fauna

The information we have found by searching local records, county records, and the annals of natural history societies is organized under the headings of invertebrates, herpetiles, birds, and mammals. Personal interviews have been used to supplement the written sources.

Invertebrates

There is no complete inventory of insects of Prince Edward County (M. Taylor, Glenora, Ont., pers. comm.). Snyder et al. (1941) listed spiders, crickets, and grasshoppers, but without locations or population estimates, so that no comparisons can be made. D. R. Barton (Department of Biology, University of Waterloo, Waterloo, Ont., unpubl. notes) studied aquatic insects along the shoreline of Lake Ontario, with some sampling sites in the Bay of Quinte.

Gerrish and Bristow (1979) estimated the association of macroinvertebrates and water plants in submerged weedbeds in 1976. Their biomass data relating particular taxa to four types of submerged plants are given in Table 1. These data should form a useful basis of comparison for further study. Snails, *Gammarus* and *Asellus* were more numerous at Adolphustown Reach than at Belleville, while the Ceratogoponidae, Trichoptera, and Naididae were higher at Belleville throughout the season, and Chironomidae, Hydra, and Planaridiiae were usually so. During the period of sampling, there was a difference in temperature of 7° (Table 1) between the water in the upper and lower bay sites. Gerrish and Bristow (1979) found that finely divided leaves supported a greater biomass of invertebrates in other sites in eastern Ontario.

Herpetiles

A survey of the herpetile fauna of Prince Edward County was carried out in 1979 (Briggs 1979). Table 2 lists herpetiles found in 1941 and 1979 for all Prince Edward County and those found in 1979 at five sites within the bay. The taxa found at these five sites were common for such habitats in Prince Edward County

TABLE 2. List of herpetiles most likely to be found along the Quinte Bay shoreline (P. Briggs, unpubl. data). A, species recorded by Snyder et al. (1941) for all Prince Edward County (+ = present, + + = common); B, species recorded by Briggs (1979) for all of Prince Edward County; C, species found at sampling sites along Quinte Bay shoreline (Briggs 1979) (1 = Baker Island, 2 = Huff Island Marsh, 3 = Big Island Marsh, 4 = Picton Bay, 5 = Hay Bay (open water)).

Species	A	B	C
Necturus maculosus maculosus (mudpuppy)	+ +	+	—
Notophthalmus viridescens viridescens (red-spotted newt)	+ +	+ +	—
Bufo americanus americanus (American toad)	+	+ +	3
Hyla crucifer crucifer (spring peeper)	+	+	—
Hyla versicolor (gray treefrog)	+	+	—
Pseudacris triseriata triseriata (western chorus frog)	+	+	—
Rana catesbeiana (bullfrog)	+	+	—
Rana clamitans melanota (green frog)	+	+ +	2,3
Rana pipiens (northern leopard frog)	+ +	+ +	2,3,4
Chelydra serpentina serpentina (snapping turtle)	+	+	—
Chrysemys picta marginata (midland painted turtle)	+	+	2,3,4
Emydoidea blandingi (blanding's turtle)	+	+	
Graptemys geographica (map turtle)	+	+	1,4,5
Sternotherus odoratus (stinkpot)	+	+	—
Natrix sipedon sipedon (northern water snake)	+	+ +	3,4
Thamnophis sirtalis sirtalis (eastern garter snake)	+ +	+ +	—

(P. Briggs, unpubl. data). There was no evidence of temporal change in the herpetile community because of a lack of quantitative data.

Birds

Data available are discussed under the headings of birds associated with Quinte Bay shorelines, breeding ducks, migratory wildfowl, and birds visiting from offshore islands.

Birds associated with the shoreline

The information given by Snyder et al. (1941), Sprague (1969), and Sprague and Weir (1984) is summarized in Table 3. Based on these qualitative data, little change in the community and limited variation in status are apparent. The pied-billed grebe has decreased from a common summer resident to an uncommon one, but no explanation for this was offered (Sprague 1969; Sprague and Weir 1984). Breeding loons and bitterns have declined, probably because of disturbed habitats (Robertson and Flood 1980). The American black duck population has decreased while those of mallard and blue-winged teal have become more common. (The changes in nesting ducks are discussed in the next section.) Red-winged blackbirds, usually associated with cattail marshes, are present in large numbers.

It is difficult to give precision to these data, as their geographical areas were either the region north of the Bay or Prince Edward County, so that some inland marshes are included.

Breeding ducks

In the 1920s, duck hunting was indicative of very large populations. Present populations are not large, and a decline was noticed in the late 1940s (Peters 1951).

While numbers declined, the community also changed during the 1950s to 1970s. In the early 1950s, the most common breeding ducks were blue-winged teal and American black duck in southern Ontario and particularly American black duck in Prince Edward County (Stirrett and Harris 1951; Stirrett 1954; Lumsden 1954a, 1954b). By 1971, breeding mallard had increased sixfold; blue-winged teal were less abundant and American black duck were only half as many as in 1951 (Collins 1979). Again, the increase in mallard was common to Prince Edward County and to southern Ontario as a whole. A difficulty with these data is a comparison of ground and aerial surveys, as blue-winged teal are less easily seen from the air (Tables 4, 5).

The decline of breeding populations has been attributed to hunting, predation, muskrat trapping, and low water levels or reduction of food plants (Peters 1951). Hunting, combined with a lack of sanctuaries, seems a likely cause because as early as the 1950s, Cringan (1958) remarked that apparently good habitats had few birds. He stated that they had only 1.2–2.0 birds per acre where 10–20 could have been expected. The habitat he described was a mixture of submerged vegetation, pools, and emergent vegetation.

Migratory wildfowl

Surveys from different dates are difficult to compare because of differences in sampling methods. The marshes of Prince Edward County are short stopover points for dabbling ducks despite artificial feeding, probably because of hunting pressure and lack of sanctuaries (Dennis and Chandler 1979). The large marshes of Big Island, Huff Island, and Hay Bay do not have as many visitors as could be expected except for large flocks of mergansers (see Table 6). The anomalous lack of waterfowl has been attributed to deteriorating habitat by R. K. Ross, (in prep.), caused by pollution, eutrophication, or extensive growth of cattails.

Migratory shorebirds are fewer than might be expected, and again, the density of cattails at marsh edges has been thought to be a cause because it reduces the number of staging sites (Strahlendorf 1979).

Visiting birds from offshore Islands

The herring gull populations fluctuate but are generally declining (Blokpoel 1977; H. Blokpoel, Canadian Wildlife Service, Ottawa, Ont., unpubl. data). This area is on the limit of their range (H. Blokpoel, pers. comm.). Nesting terns have also declined (Blokpoel 1977; H. Blokpoel, unpubl. data). Caspian Terns have not been common nesters in this part of the Lake Ontario basin, although they nest at Pigeon Island — they do not appear to have changed significantly in numbers (Blokpoel 1977).

Ring-billed gulls have a large nesting population which has been increasing rapidly since 1960 (Ludwig 1974; Blokpoel 1977; H. Blokpoel, unpubl. data). Double-crested cormorants were not common in 1941 (Snyder et al. 1941), were rare in the 1960s and early 1970s, and are now fairly common (Sprague and Weir 1984). Their nesting sites include Little Galloo Island, Scotch Bonnet Island, and Pigeon Island, and while the population on the islands had dwindled until the late 1970s, there was a dramatic increase by 1980 (H. Blokpoel, unpubl. data). The colony on Little Galloo Island increased by 200% from 1977 to 1981 (D. V. Weseloh, Canadian Wildlife Service, Ottawa, Ont., pers. comm.; Scharf and Shugart 1981).

Changes in breeding success and breeding behaviour have been linked to pollutants such as DDT in herring gulls on Scotch Bonnet Island; after a marked decline, the ban on DDT was reflected by recovery in numbers and possibly behaviour (G. Fox, Canadian Wildlife Service, Ottawa, Ont., pers. comm.). Other piscivores show a similar pattern (Scharf and

TABLE 3. Summary of status of birds associated with shoreline of Prince Edward County from Snyder et al. (1941), Sprague (1969), and Sprague and Weir (1984), and breeding status along Quinte Bay shoreline as recorded for the Ontario Breeding Bird Atlas Survey (Sprague 1983). Taxonomy of birds according to American Ornithologists' Union nomenclature (1982). S, spring; F, fall; Fr., fairly; isl., islands; no., numbers.

	Snyder et al. (1941)		Sprague (1969)		Sprague and Weir (1984)		Breeding status (Sprague 1983)		
Species	As migrant	As summer resident	As migrant	As summer resident	As migrant	As summer resident	Prob.	Conf.	Recorded abundance[a]
Red-throated loon (*Gavia stellata*)	Rare, S,F		Rare, S,F		Rare, S,F				
Arctic loon (*Gavia arctica*)					One record, S				
Common loon (*Gavia immer*)	Regular, S	Recorded breeding		Fr. common, breeding	Common, regular, S,F	Uncommon		+	1,1,1
Pied-billed grebe (*Podilymbus podiceps*)	Common, S,F	Common breeder	Uncommon, S,F	Uncommon	Regular, S,F	Uncommon	+		2,1,2
Horned grebe (*Podiceps auritus*)	Fr. common		Fr. common		Fr. common				
Red-necked grebe (*Podiceps grisegena*)	S,F		Rare, S,F		Rare, S,F				
Eared grebe (*Podiceps nigricollis*)					Very rare, S,F				
Double-crested cormorant (*Phalacrocorax auritus*)	Regular, S,F			Uncommon, nearby isl.		Fr. common, nearby isl.			
American bittern (*Botaurus lentiginosus*)		Common		Common		Fr. common		+	2,3,2,2,2
Least bittern (*Ixobrychus exilis*)		Fr. common		Fr. common		Rare, uncommon	+		2
Great blue heron (*Ardea herodias*)	S,F	Fr. common		Fr. common		Fr. common, some overwinter		+	3,3,3
Green-backed heron (*Butorides striatus*)				Uncommon	Uncommon, regular, S,F	Uncommon		+	2,2,1
Black-crowned night-heron (*Nycticorax nycticorax*)		Uncommon, irregular		Nesting on nearby isl.		Rare, regular, nearby isl.			
Tundra swan (*Cygnus columbianus*)	Rare, irregular, S,F		Uncommon, regular, S,F		Fr. common, regular, S,F				
Snow goose (*Chen caerulescens*)	Rare, irregular, F		Regular, F		Rare, S,F, regular				
Brant (*Branta bernicla*)	Rare, irregular				Common, S; uncommon, F				
Canada goose (*Branta canadensis*)	Regular, S,F		Common, regular, S,F		Abundant, regular, S,F	Rare, some overwinter		+	
Wood duck (*Aix sponsa*)	S,F	Reduced no., regular		Seriously decreased no.	Fr. common, S,F	Fr. common		+	2,2
Green-winged teal (*Anas crecca*)	Fr. common, S,F		Fr. common, S,F		Fr. common, S; uncommon, F	Uncommon	+		1,1
American black duck (*Anas rubripes*)	Most common duck, S,F	Most common duck		Declining in no., some overwinter	Common, S,F	Uncommon, declining no.	+		2,2,1,1
Mallard (*Anas platyrhynchos*)	S,F	Not known		Common, some overwinter	Common, S,F	Fr. common		+	3,3,3,3,2, 3,2
Northern pintail (*Anas acuta*)	Fr. common, S,F		Rare, S,F	Rare	Common, S,F	Uncommon to rare	+		1,1

TABLE 3. *(Continued)*

Species	Snyder et al. (1941)		Sprague (1969)		Sprague and Weir (1984)		Breeding status (Sprague 1983)		
	As migrant	As summer resident	As migrant	As summer resident	As migrant	As summer resident	Prob.	Conf.	Recorded abundance[a]
Blue-winged teal (*Anas discors*)	Common, F	Fr. common		Common	Fr. common, S,F	Fr. common		+	3,3,3,2,2
Northern shoveler (*Anas clypeata*)	Rare, S,F		Rare, regular, S,F		Uncommon, S; casual, F	Rare	+		1,1
Gadwall (*Anas strepera*)	Rare, F		Rare, F		Fr. common, S,F	Fr. common	+		1,1
American wigeon (*Anas americana*)	Rare, S,F		Fr. common, S,F		Uncommon, S; uncommon, F	Rare			
Canvasback (*Athya valisineria*)	Rare, regular, S,F, formerly vast flocks		Uncommon, regular, S,F		Common, S; uncommon, F				
Redhead (*Aythya americana*)	Rare, S,F formerly vast flocks		Common, S,F		Uncommon, S,F				
Ring-necked duck (*Aythya collaris*)	Fr. common, regular, S,F		S,F		Uncommon, S; very rare, F				
Greater scaup (*Aythya marila*)	Most common of non-breeding ducks, S,F, no. reduced		Most common of non-breeding ducks		Common, S; abundant, F	Fr. common in winter			
Lesser scaup (*Aythya affinis*)	Fr. common, S,F		S,F		Fr. common, S; uncommon, F				
Common eider (*Somateria mollissima*)					Very rare, F				
King eider (*Somateria spectabilis*)	Rare, F		Rare, F		Rare, F				
Harlequin duck (*Histrionicus histrionicus*)					Casual, F				
Oldsquaw (*Clangula hyemalis*)	F	Some overwinter	Common, S,F	Some overwinter	Abundant, S,F	Abundant in winter			
Black scoter (*Melanitta nigra*)					Rare, S; uncommon, F				
Surf scoter (*Melanitta) perspicillata*)					Uncommon, S,F				
White-winged scoter (*Melanitta fusca*)	Uncommon, regular, S,F		Regular, S,F	Some overwinter	Fr. common, S,F				
Barrow's goldeneye (*Bucephala islandica*)					One winter record				
Common goldeneye (*Bucephala clangula*)	Fr. common, S,F		Common, S,F	Some overwinter	Very common, S,F	Very common in winter			
Bufflehead (*Bucephala albeola*)	Rare, regular, S,F		Fr. common, S,F		Abundant, S,F	Common in winter			

TABLE 3. *(Continued)*

Species	Snyder et al. (1941)		Sprague (1969)		Sprague and Weir (1984)		Breeding status (Sprague 1983)		
	As migrant	As summer resident	As migrant	As summer resident	As migrant	As summer resident	Prob.	Conf.	Recorded abundance[a]
Hooded merganser (*Lophodytes cucullatus*)	Regular, S,F		Fr. common, S,F		Uncommon, S; rare, F		+		
Common merganser (*Mergus merganser*)	Fr. common, S,F		Very common, S,F		Very common, S; common, F	Common in winter		+	
Red-breasted merganser (*Mergus serrator*)	Common, S,F		Common, S,F		Common, S; uncommon, F	Recent in summer			
Ruddy duck (*Oxyura jamaicensis*)	Rare, irregular, S,F		Rare, regular, S,F		Very rare, S; rare, F				
Northern harrier (*Circus cyaneus*)	Most common hawk	Most common hawk	Common	Common, some overwinter	Common, S,F	Fr. common		+	1,2,3,3,2, 2,1
Yellow rail (*Coturnicops noveboracensis*)					Regular, very rare, S				
King rail (*Rallus elegans*)		Present in marshes		Present in marshes		Rare, irregular			
Virginia rail (*Rallus limicola*)		Common in marshes		Common in marshes		Fr. common		+	3,3,1
Sora (*Porzana carolina*)		Common in marshes		Common in marshes		Fr. common		+	3,2,2,2
Common moorhen (*Gallinula chloropus*)		Common in marshes		Common		Fr. common	+		3,3
American coot (*Fulica americana*)					Fr. common, S,F	Occasionally nests			
Killdeer (*Charadrius vociferus*)		Common		Common	Common, S; abundant, F	Common		+	3,4,4,4,3, 3,3,2
Spotted sandpiper (*Actitus macularia*)		Common		Common		Fr. common		+	3,3,3,3,3, 2
Upland sandpiper (*Bartramia longicauda*)		Fr. common		Present		Fr. common		+	3,3,2,2,1
Common snipe (*Gallinago gallinago*)	S,F	Uncommon, formerly plentiful	Common	Common		Fr. common		+	3,3,3,2
American woodcock (*Scolopax minor*)	Rare	Rare, formerly common		Fr. common		Fr. common		+	2,3,3,3,3, 2
Wilson's phalarope (*Phalaropus tricolor*)		Rare		Observed		Rare	+		1
Ring-billed gull (*Larus delawarensis*)		Visitor, mainly S,F		Common, nesting on nearby isl.	Very common, S,F	Very common			
Herring gull (*Larus argentatus*)		Visitor, all year		Common, nesting on nearby isl.	Abundant, S,F	Common, abundant in winter			
Caspian tern (*Sterna caspia*)		Uncommon, S,F		Common, nesting on nearby isl.	Common, S,F	Common			
Common tern (*Sterna hirundo*)		Common, nesting on nearby isl.		Common, nesting on nearby isl.	Uncommon, S; fr. common, F	Uncommon			

TABLE 3. *(Concluded)*

Species	Snyder et al. (1941)		Sprague (1969)		Sprague and Weir (1984)		Breeding status (Sprague 1983)		
	As migrant	As summer resident	As migrant	As summer resident	As migrant	As summer resident	Prob.	Conf.	Recorded abundance[a]
Forster's tern (*Sterna forsteri*)					Occasional, S	One summer record			
Black tern (*Chlidonias niger*)		Common		Common		Fr. common		+	3,3
Belted kingfisher (*Ceryle alcyon*)		Present		Common, some overwinter	Fr. common, S,F	Uncommon		+	2,3,3,2,2, 2,2,1
Eastern phoebe (*Sayornis phoebe*)		Regular		Fr. common, regular	Fr. common, S,F	Uncommon		+	2,2
Eastern kingbird (*Tyrannus tyrannus*)		Common		Common	Common, S; very common, F	Fr. common		+	3,3,3,3,3, 3,2
Purple martin (*Progne subis*)		Fr. common		Fr. common	Very common, F	Common		+	3,3,3,3,3, 3,2
Tree swallow (*Tachycineta bicolor*)		Common		Common	Abundant, S,F	Common		+	3,4,4,4,4, 3,4,3
Northern rough-winged swallow (*Stelgidopteryx serripennis*)		Rare		Fr. common	Common, S; fr. common, F	Fr. common		+	3,2,2,2,1
Bank swallow (*Riparia riparia*)		Common, irregularly distributed		Common	Uncommon, S; fr. common, F	Fr. common		+	3,2
Cliff swallow (*Hirundo pyrrhonota*)		Present		Uncommon	Uncommon, S,F	Uncommon		+	2,1
Barn swallow (*Hirundo rustica*)		Common		Very common	Very common, S; abundant, F	Common		+	3,3,3,3,3, 3,4,3
Sedge wren (*Cistothorus platensis*)		Irregular		Uncommon		Rare to uncommon			
Marsh wren (*Cistothorus palustris*)		Common in marshes		Common in marshes		Fr. common	+		3,4
Common yellowthroat (*Geothlypis trichas*)		Common, breed on many marsh borders		Very common in marsh areas	Common, S,F; abundant, S,F	Fr. common, abundant		+	3,3,2,3,2
Red-winged blackbird (*Agelaius phoeniceus*)		Very common in marshes		Very common in marshes	Very abundant, S,F	Abundant		+	3,5,5,4,4, 4,5,3

[a] 1, 1 pair present; 2, 2–10 pairs present; 3, 11–100 pairs present; 4, 101– 1000 pairs present; 5, 1001–10 000 pairs present (Eagles and Cadman 1981).

Shugart 1981). Interspecific differences could be due to differences between diets composed wholly of fish and those including terrestrial food.

Although these bird populations do not depend on the Bay of Quinte for their breeding success, they may be important in the ecology of the bay as fish predators.

Mammals (taxonomy according to Banfield 1974)

Muskrats (*Ondatra zibethicus* Kuhl) and beavers (*Castor canadensis* Kuhl) are the important mammals of the Bay of Quinte wetlands, although one would also expect mice, voles, moles, raccoons, and perhaps mink there. Beaver increased in the 1930s (Snyder et al. 1941), as they did in much of southern Ontario. They are more common in the marshes than along the rocky shores, although they can occasionally be seen beside the Glenora ferry. Shores backed by fields rather than edible trees limit their numbers, which are not so dense as in wooded parts of the Canadian Shield north of the bay.

Muskrats are trapped in the bay and records of furs sold (and sometimes of the density of muskrat houses) date back to the 1930s. In 1977, Palilionis compared density in Big Island marsh, Hay Bay, and marshes on the Rideau River (Table 7). All were considered relatively low. At least 12 trappers use Hay Bay and, in 1975–79, trapped 60–400 muskrats per year.

The trapping records from 1961 to 1976 showed a fluctuating

TABLE 4. Estimate of pairs of main nesting species of ducks at Huff Island and Big Island marshes from aerial and ground surveys for 1951–58 and ground survey for 1958 (from Cringan 1958). NS, not surveyed.

	Aerial surveys								
Species	1951: May 31	1952: May 16	1953: July 13	1954: May 16	1955: May 13	1956: May 14–15	1957: May 13	1958	Ground survey, 1958
Huff Island Marsh									
Blue-winged teal	2	1	0	0	NS	0	1	0	27
Mallard	1	0	10	6	NS	5	16	12	17
Black duck	3–5	3–5	12–23	4–7	NS	2–3	6–11	7	11
Total	6–8	4–6	22–33	10–13	NS	7–8	23–28	19	55
Big Island Marsh									
Blue-winged teal	2	0	1	0	3	0	1	0	12
Mallard	0	1	5	1	4	5	6	3	15
Black duck	1	1	1–2	3–6	13–15	1–2	0	9	12
Total	3	2	7–8	4–7	20–22	6–7	7	12	39

TABLE 5. Total number of ducks observed for three main nesting species in Huff Island, Big Island, and Hay Bay marshes using aerial or ground surveys. Except for Cringan's (1958) ground survey, all other surveys took place on one day. NS, not surveyed.

		Aerial surveys								
Species	Ground survey, Stirrett and Harris (1951)	Lumsden (1951)	Lumsden (1952)	Lumsden (1953)	Lumsden (1954b)	Bittle (1956)	Cringan (1958)	Ground survey, Cringan (1958)	Aerial survey, Bittle (1960)	Ground survey, J. M. Collins[a]
Huff Island Marsh										
Mallard	NS	0	0	11	7	8	24	34	3	NS
Black duck	NS	3	5	23	7	7	14	22	9	NS
Blue-winged teal	NS	4	1	0	0	0	0	54	2	NS
Big Island Marsh										
Mallard	1	0	2	5	1	5	6	30	15	2
Black duck	2	1	1	2	6	2	9	24	13	0
Blue-winged teal	9	2	0	2	0	0	0	24	0	4
Hay Bay Marsh										
Mallard	NS	0	2	2	8	7	NS	NS	1	9
Black duck	NS	5	0	3	0	13	NS	NS	3	2
Blue-winged teal	NS	6	2	2	8	0	NS	NS	0	8

[a] Data obtained from G. McCullough (Canadian Wildlife Service, London, Ont.).

population (Palilionis 1977), although these data can reflect fur prices as well as density. It is normal for muskrat numbers to fluctuate (Errington et al. 1963; Weller 1981) and the causes have variously been suggested to be (1) a cycling population, (2) higher mortality in years with droughts or unusually cold winters, or a combination of dry and cold conditions in winter, (3) lack of food plants, particularly *Typha*, possibly as a result of changed water levels, and (4) overintensive trapping.

It is not possible to assess the causes of the fluctuations in the Bay of Quinte populations, although Palilionis (1977) favoured a combination of low water levels and severe winters as the cause of declines in 1963–68 and 1972–77 (cf. Sly 1986). There are no records of "eat-outs" of cattails such as those recorded in Iowa (Weller 1981) in which the decimation of the plants caused a change from emergent marsh to open water. In fact, Palilionis (1977) commented, when the population was relatively low, that Big Island appeared to be the ideal habitat with plenty of food and a mixture of open water and emergents.

Discussion

There is a dearth of accurate information about the fauna of the wetlands and shores during the past 50 yr, and existing data are hard to compare because of anomalies of sampling. The only obvious trends were (1) a diminution of numbers of breeding ducks, (2) a change in the community of ducks from blue-winged teal and American black duck to mallard, (3) a diminution of offshore fish-eating birds, followed by increased visiting of double-crested cormorants and ring-billed gulls, (4) a slight increase in beavers since the 1930s, and (5) fluctuating populations of muskrats.

Changes in habitat have included drainage. Whillans (1982) measured extensive loss of wetlands along the Lake Ontario shore west of Prince Edward County due to road making, agriculture, housing, etc., and while the Bay of Quinte has probably not changed to a similar extent, there has been some loss. Within the marshes, there is evidence of a loss of stands of wild rice, wild celery, and sago pondweed, which are all food for ducks. Carp have increased in the bay and may be partly responsible for this change; carp caught in 1978 had 10 plant species in their stomachs, including seeds of wild rice and of two species of pondweed (Powles et al. 1983). There are now extensive stands of cattails, used as food by muskrats. Paleoecological evidence suggests that the cattail stands spread in

TABLE 6. Number of migrating ducks in Quinte Bay recorded by surveys of the Canadian Wildlife Service, Ottawa, Ont. Data for the 1970 survey were obtained by D. G. Dennis and R. E. Chandler, while the 1977 survey was conducted by K. Ross. 1970–71: A, Muscote Bay, Aug. 31 to Dec. 21 (8 samples); B, Hay Bay, Aug. 31 to Dec. 21 (8 samples). 1977 (spring flights): C, Murray Canal to Belleville, Mar. 25 to Apr. 30 (3 samples); D, Belleville to Deseronto (Muscote Bay), Mar. 11 to Apr. 30 (4 samples); E, Long Reach (Hay Bay), Mar. 25 to May 25 (4 samples); F, Picton Bay to Adolphus Reach, Mar. 25 to Apr. 30 (3 samples), 1977 (fall flights): G, Belleville to Deseronto (Muscote Bay), Aug. 29 (1 sample); H, Long Reach (Hay Bay), Aug. 29 to Nov. 2 (2 samples); I, Picton Bay to Adolphus Reach, Nov. 6 to Dec. 3 (2 samples).

	1970		Spring 1977				Fall 1977		
Species	A	B	C	D	E	F	G	H	I
Canada goose *(Branta canadensis)*	146	72	—	43	20	20	—	—	—
Wood duck *(Aix sponsa)*	37	2	—	—	—	—	—	—	—
Green-winged teal *(Anas crecca)*	122	89	—	—	—	—	—	—	—
American black duck *(Anas rubripes)*	723	205	—	56	—	4	—	—	23
Mallard *(Anas platyrhynchos)*	1 937	585	—	21	—	6	5	—	6
Northern pintail *(Anas acuta)*	7	4	—	20	—	3	—	—	—
Blue-winged teal *(Anas discors)*	53	44	—	1	1	—	—	20	—
Gadwall *(Anas strepera)*	—	4	—	—	—	—	—	—	—
American wigeon *(Anas americana)*	1	—	—	7	—	—	12	—	—
Canvasback *(Aythya valisineria)*	85	1	—	—	6	—	—	—	—
Ring-necked duck *(Aythya collaris)*	2	15	—	—	—	—	—	—	—
Scaup *(Aythya* spp.)	877	489	—	43	28	1 519	—	23	7
Oldsquaw *(Clangula hyemalis)*	—	—	—	—	—	12	—	—	—
Common goldeneye *(Bucephala clangula)*	8	74	16	160	60	729	—	48	193
Bufflehead *(Bucephala albeola)*	20	8	—	—	5	178	—	—	—
Mergansers	14 209	450	298	2 262	647	308	—	4	116
Common moorhen *(Gallinula chloropus)*	7	—	—	—	—	—	—	—	—
American coot *(Fulica americana)*	13	1	—	—	—	—	—	—	—
Unknown	1 076	112	—	277	36	2 149	2	30	20
Total	25 520	2 149	314	2 890	803	4 928	17	125	365

conjunction with forest clearance and increased runoff (Terasmae and Mirynech 1964), starting in the eighteenth century. Where silting occurs, a slow succession towards fen carr and swamp forest could be expected.

The diminution of breeding ducks could be related to loss of food plants, but hunting and a lack of sanctuaries may be responsible. This seems a more likely explanation because Cringan (1958) remarked on the paucity of birds in good habitats as early as the 1950s. Dabbling ducks are most dense in habitats consisting of equal areas of open water and emergent plants (Kaminski and Prince 1981), and large areas of Hay Bay provide this mixture.

The change of balance between mallards and other ducks is part of a general phenomenon in southern Ontario, but can reflect local changes of water level. Blue-winged teal tend to use the upper parts of marshes, American black ducks the lower, and mallards generally increase in particularly wet years (Weller 1981). Increased density of cattails may also have reduced the suitable sites for nests in the wetter areas. Reduction in numbers of loons and bitterns is likely to be caused by disturbance during the breeding season, for example by boat traffic (Robertson and Flood 1980).

TABLE 7. Estimates of muskrat populations at Big Island and Hay Bay in the Bay of Quinte and in Rideau Marshes. Data from Palilionis (1977). Five muskrats per house were assumed.

Marsh	Houses per acre	Total population
Rideau	0.6370	3185
Big Island	0.4625	3496
Hay Bay	0.4103	4852

Predation of fish in the bay is influenced by birds that breed on the islands in Lake Ontario. Terns and gulls have shown behavioural changes and experienced breeding failures that have been attributed to pollution (Gilman et al. 1977), but have recently begun to breed successfully again. The change in breeding success began in 1978 following legal restrictions on pesticides such as DDT (G. Fox, Ottawa, Ont., pers. comm.). Double-crested cormorants, which are also piscivores, have been visiting the bay in larger numbers in recent years and may show the same reaction to pollutants (D.V. Weseloh, Ottawa, Ont., pers. comm.). The increase of cormorants has been general in the Great Lakes, but the greatest population growth is on Little Galloo Island (Scharf and Shugart 1981).

The number of beavers is low in comparison with that in neighbouring parts of eastern Ontario, where there is less farming and where there are more forested shorelines. They appear to have had little impact on water levels in the marshes.

Muskrat populations have not been reported to be dense and there is no evidence of them having "eaten-out" their main food, the cattail. Their numbers have fluctuated temporally but it is not possible to distinguish the effects of microclimatic change, water levels, and trapping.

The mammals and birds interact in the marshes, as muskrats keep the channels and the areas around their houses open, providing a more mixed habitat than dense cattail stands. Birds such as mallards and terns may nest on top of old muskrat houses.

Apart from the indirect effects of changes in food plants and lowered plant diversity, eutrophication does not appear to have greatly changed the fauna of the wetlands. Drainage, hunting, trapping, and recreational traffic appear to have had greater impacts. If future trends are to be investigated, regular long-term sampling on a consistent basis should be instituted.

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References

AMERICAN ORNITHOLOGISTS' UNION. 1982. Committee on classification and nomenclature. 1982. Check-list of North American birds. Supplement to the Auk Vol. 99, No. 3, July 1982. 16 p.

BANFIELD, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Downsview, Ont. 438 p.

BITTLE, W. W. 1956. Waterfowl breeding ground survey. Tweed District. Internal Report, Ontario Department of Lands and Forests, Division of Fish and Wildlife (Ministry of Natural Resources Library, Toronto, Ont.). 3 p.

1960. Waterfowl production survey. Tweed District. Internal Report, Ontario Department of Lands and Forests, Division of Fish and Wildlife (Ministry of Natural Resources Library, Toronto, Ont.). 7 p.

BLOKPOEL, H. 1977. Gulls and terns nesting in Northern Lake Ontario and the Upper St. Lawrence River. Progress notes, No. 75. Canadian Wildlife Service, Ottawa, Ont. 12 p.

BRIGGS, P. 1979. A preliminary report on the 1979 survey of reptiles and amphibians of Prince Edward County. Reptile Breeding Foundation, Milford, Ont. 14 p.

COLLINS, J. M. 1979. The relative abundance of ducks breeding in Southern Ontario in 1951 and 1971, p. 32–44. *In* H. Boyd [ed.] CWS studies in Eastern Canada 1969–1973. CWS Rep. Ser. No. 29.

CRINGAN, A. T. 1958. Waterfowl production in the large marshes of Prince Edward County. Report on Preliminary Investigations, Ann Arbor, MI. 112 p.

CROWDER, A. A., AND J. M. BRISTOW. 1986. Aquatic macrophytes in the Bay of Quinte, 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

DENNIS, D. G., AND R. E. CHANDLER. 1979. Waterfowl use of the Ontario shorelines of the Southern Great Lakes region during migration, p. 58–65. *In* H. Boyd [ed.] CWS waterfowl studies in Eastern Canada 1969–1973. CWS Rep. Ser. No. 19.

EAGLES, P. F. J., AND M. D. CADMAN. 1981. Ontario breeding bird atlas. Ontario Breeding Bird Atlas Management Committee, Toronto, Ont. 28 p.

ERRINGTON, P. L., R. J. SIGLIN, AND R. C. CLARK. 1963. The decline of a muskrat population. J. Wildl. Manage. 27: 1–8.

GERRISH, N., AND J. M. BRISTOW. 1979. Macroinvertebrate associations with aquatic macrophytes and artificial substrates. J. Great Lakes Res. 5: 69–72.

GILMAN, A. P., G. A. FOX, D. B. PEAKALL, S. M. TEEPLE, T. R. CARROLL, AND G. T. HAYNES. 1977. Reproductive parameters and contaminant levels of Great Lake Herring Gulls. J. Wildl. Manage. 41: 458–468.

KAMINSKI, R. M., AND H. H. PRINCE. 1981. Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. J. Wildl. Manage. 45: 1–15.

LUDWIG, J. P. 1974. Recent changes in the Ring-billed Gull population and biology in the Laurentian Great Lakes. Auk 91: 575–594.

LUMSDEN, H. G. 1951. Waterfowl breeding stock in Tweed District. Internal Report, Ontario Department of Lands and Forests, Division of Fish and Wildlife (Ministry of Natural Resources Library, Toronto, Ont.). 4 p.

1952. Waterfowl breeding stock in Quinte District. Fish and Wildlife Management Report, Ontario Department of Lands and Forests, Division of Fish and Wildlife, No. 11: 3 p.

1953. Waterfowl breeding stock in Quinte District. Internal Report, Ontario Department of Lands and Forests, Division of Fish and Wildlife (Ministry of Natural Resources Library, Toronto, Ont.). 3 p.

1954a. Waterfowl breeding ground survey Tweed District. Internal Report, Ontario Department of Lands and Forests, Division of Fish and Wildlife (Ministry of Natural Resources Library, Toronto, Ont.). 5 p.

1954b. Waterfowl breeding stock in Tweed District. Internal Report, Ontario Department of Lands and Forests, Division of Fish and Wildlife (Ministry of Natural Resources Library, Toronto, Ont.). 3 p.

MALTBY, L. S., G. B. MCCULLOUGH, AND E. Z. BOTTOMLEY. 1983. Baseline studies of 35 selected southern Ontario wetlands, 1983. Canadian Wildlife Service, Environment Canada, Ontario Region, Ottawa, Dec. 1983.

PALILIONIS, A. P. 1977. A study of Big Island, Hay Bay and Rideau marshes in relation to marsh management. Report for Ministry of Natural Resources, Napanee District, Fish and Wildlife Branch. 64 p.

PETERS, W. A. 1951. Feathers preferred. McClelland and Stewart, Toronto, Ont.

POWLES, P. M., H. R. MACCRIMMON, AND D. A. MACRAE. 1983. Seasonal feeding of Carp, Cyprinus carpio, in the Bay of Quinte watershed, Ontario. Can. Field-Nat. 97(3): 293–298.

ROBERTSON, J. R., AND N. J. FLOOD. 1980. Effects of recreational use of shorelines on breeding bird populations. Can. Field-Nat. 94(2): 131–138.

SCHARF, W. C., AND G. W. SHUGART. 1981. Recent increases in double-crested Cormorants in the United States Great Lakes. Am. Birds 35(6): 910–911.

SLY, P. 1986. Review of postglacial environmental changes and cultural impacts in the Bay of Quinte, p. 7–26. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

SNYDER, L. L., E. B. S. LOGIER, T. B. KURATA, F. A. URQUHART, AND J. F. BRIMLEY. 1941. A faunal investigation of Prince Edward County, Ontario. The University of Toronto Press, Toronto, Ont.

SPRAGUE, T. 1969. Birds of Prince Edward County. The Picton Gazette Publishing Co. Ltd., Picton, Ont. 215 p.

1983. Master Cards for Ontario Breeding Bird Atlas Survey, Zone 18, Block 00.

SPRAGUE, R. T., AND R. D. WEIR. 1984. The birds of Prince Edward County. 2nd ed. The Kingston Field Naturalists, Kingston, Ont. 206 p.

STIRRETT, G. M. 1954. Waterfowl breeding ground survey in southern Ontario, 1954. Can. Wildl. Serv. Rep. No. 396: 4 p.

Stirrett, G. M., and R. D. Harris. 1951. Preliminary report waterfowl breeding survey in southern Ontario in 1951. Can. Wildl. Serv. Rep. No. 382: 13 p.

Strahlendorf, P. W. 1979. Migrant shorebird ecology. Prepared for Parks Branch, Ministry of Natural Resources, Napanee District, Napanee, Ont. 96 p.

Terasmae, J., and E. Mirynech. 1964. Post-glacial chronology and the origin of deep lake basins in Prince Edward County, Ontario. Great Lakes Research Division, Publication 11, University of Michigan, Ann Arbor, MI.

Weller, M. W. 1981. Freshwater marshes. Ecology and wildlife management. University of Minnesota Press, Minneapolis, MN.

Whillans, T. H. 1982. Changes in marsh area along the Canadian shore of Lake Ontario. J. Great Lakes Res. 8: 570–577.

Fish Populations of the Bay of Quinte, Lake Ontario, Before and After Phosphorus Control[1]

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Hurley, D.A. 1986. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C.K. Minns, D.A. Hurley, and K.H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

The abundance and distribution of the major fish species in the Bay of Quinte were determined, using both mobile and static gear, in the years prior to and following the significant reduction in nutrient inputs that occurred in 1977–78. Although year-to-year variability in their numbers was high, some of the major species, such as alewife (*Alosa pseudoharengus*), white perch (*Morone americana*), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum vitreum*), showed significant shifts in abundance that were evidently more related to a climatic anomaly and to predator–prey interactions than to changes in nutrient concentrations. The fish community of the bay has changed from a percichthyid–clupeid dominated one during the 1960s and 1970s to one where percids are now more abundant and percichthyids and clupeids are reduced.

On a déterminé le nombre et la répartition des principales espèces de poisson dans la baie de Quinte à l'aide d'engins mobiles et fixes avant et après l'importante baisse de l'apport de bioéléments en 1977–1978. La variabilité du nombre d'une année à l'autre était élevée, mais certaines des principales espèces comme le gaspareau (*Alosa pseudoharengus*), le baret (*Morone americana*), la perchaude (*Perca flavescens*) et le doré jaune (*Stizostedion vitreum vitreum*) ont présenté d'importantes variations numériques qui étaient manifestement plus liées à une anomalie climatique et aux interactions prédateur–proie qu'aux changements des concentrations de bioéléments. Dominée par les percichthyidés et les clupéidés au cours des années 1960 et 1970, la communauté piscicole de la baie est maintenant composée principalement de percidés et d'un nombre réduit de percichtyidés et de clupéidés.

Introduction

One of the major goals of Project Quinte was to examine the effect of trophic state, in a nutrient loading context, on the structure, composition, and diversity of aquatic communities (Anonymous 1981). With respect to the fish community, the objective was to compare the structure, diversity, and production before and after phosphorus control.

In light of this goal and objective, the primary purpose of this paper is to provide a compendium of information on the fish species of the bay before and after phosphorus control. A secondary purpose is to relate observed changes in fish species to possible causes such as nutrient concentrations, weather anomalies, piscivore abundance, and exploitation.

In a previous paper, Hurley and Christie (1977) described the fish community of the bay when it was in a degraded state, one we characterized by large numbers of small-sized, or stunted, species with relatively short life spans but with high reproductive potential. Christie and Scott (1985) elaborated on this theme further, while Minns and Hurley (1986) examined the production of white perch,[2] one of the major species in the bay.

It was the contention of Christie (1973) and Hurley and Christie (1977) that the abundance of piscivores was a key factor in maintaining a balanced fish community, i.e. one where one or two species of planktivores or benthivores did not dominate the community. The thesis of these authors was that eutrophication produced a stress that inhibited the ability of large piscivores to compete successfully, and as a consequence, smaller, short-lived species proliferated. A comparable situation developed in Lake Wingra where eutrophication, habitat alteration, and introduction of exotic species resulted in the decline of the native fish predators, while species of panfish increased in number and became stunted (Baumann et al. 1974).

In the Bay of Quinte, however, reductions in nutrient inputs and the effects of a weather anomaly have resulted in a reversal of this trend. The dramatic return of piscivorous walleye in the late 1970s, and the contemporaneous decline in white perch, probably caused by a winter-kill, have resulted in reduction of small-sized species and an increase in the growth rate of white perch.

The fish community, therefore, has responded in a relatively short time frame to the relaxation of some of the stresses that had caused its degradation. Whether or not this current structure can be maintained will depend on the continued production of large piscivores (Christie and Scott 1985), and ultimately on the maintenance of reduced nutrient inputs.

Methods

Sampling Locations

The Bay of Quinte (Fig. 1) can be morphologically separated into three distinct zones (Sly 1986). The upper bay from the Trent River to Deseronto is relatively flat-bottomed with a mean depth of 3.2 m. The middle bay from Deseronto to Glenora contains Long Reach, Hay Bay, and a broadened area from Picton to Glenora. The mean depth of Long Reach is 6.3 m and of Hay Bay is 1.9 m. The lower bay extends from Glenora to

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[1] Contribution 85-01, Ontario Ministry of Natural Resources, Fisheries Branch, Maple, Ont. L0J 1E0.

[2] Scientific names of fish species are given in Table 1.

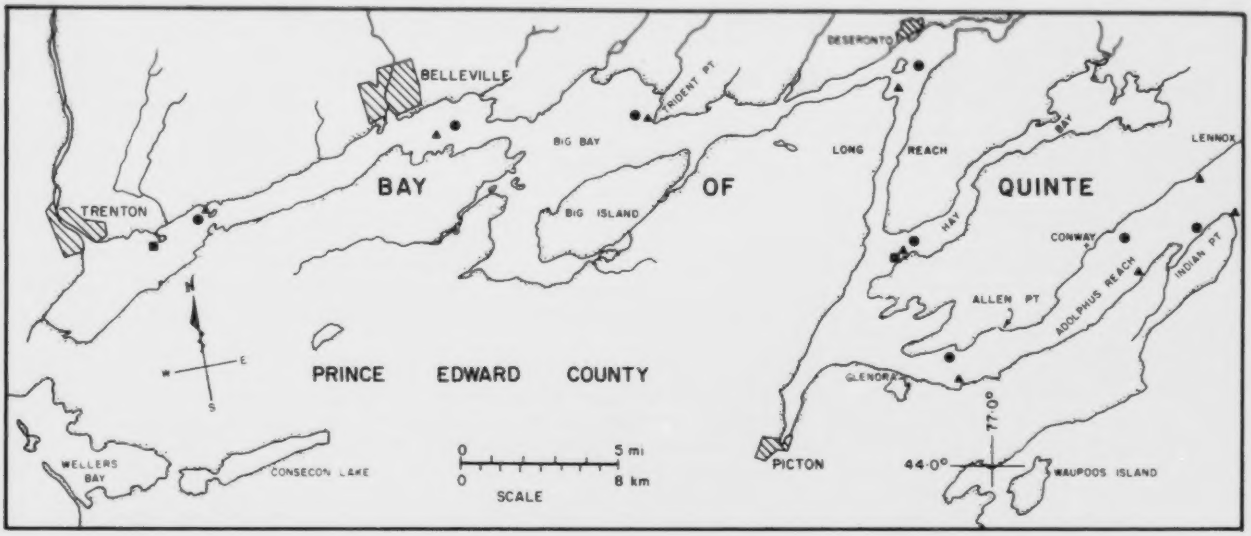

FIG. 1. Bay of Quinte showing sites of trawl drags (●), gillnet sets (▲), and trap nets (■).

Adolphus Reach and has a mean depth of 23.8 m. The three zones exhibit marked differences in temperature profiles primarily because of their different mean depths; sampling locations were chosen to represent these zones. The upper bay was always the warmest and the lower bay the coldest zone.

Sampling Gear

Four types of sampling gear were used: bottom trawls and gill nets for sampling deeper offshore sections of the bay, trap nets for shallower nearshore areas, and beach seines for selected areas along the shore. Each type of gear was suited to examine certain segments of the fish populations. Each also has its degree of selectivity so that a combination of gear types allows a more integrated understanding of the nature of fish populations in any location within the bay.

Bottom trawl

A 3/4 Western bottom trawl, 19 m long with 6-m wings and 1.3-cm stretched mesh in the cod-end, was used each month from May through September and dragged over a distance of 400 m at a speed of 1.1 $m \cdot s^{-1}$. Seven locations were fished from 1972 to 1974 and an eighth was added near Indian Point from 1975 to 1980 (Fig. 1). In 1981 and 1983, only three sites were fished, Big Bay, Hay Bay, and Conway. No fishing was done in 1982. The depth of the trawl drags was 5 m in the upper bay between Trenton and Deseronto, 7 m at Hay Bay, 18 m at Glenora and Indian Point, and 22 m at Conway. The 400-m drag was used as the unit of effort.

Bottom trawl drags were limited to areas where the bottom is relatively smooth and free from obstructions. Trawl doors and warps tend to herd fish but that reaction depends on the degree of visibility of the net (Blaxter et al. 1964). With Secchi disc values of between 90 and 300 cm in the Bay of Quinte, the trawl would be invisible at a distance of a few metres in the water.

Beach seine

A limited number of seine hauls were made on an irregular basis during June, July, and August throughout the bay, primarily to census the fish populations along the shoreline. A bag seine of 9-m length, 1.8-m depth, and 0.3-cm^2 "Delta" mesh was used to sweep selected shore locations between 18:00 and 06:00.

Bottom gill net

Between 1972 and 1974, an experimental gill net containing a series of graded mesh sizes was set once each month (May–August) at seven sites. After 1975, two additional sites were added near Indian Point (Fig. 1). A similar net had been fished at one location in Hay Bay since 1958. After 1980 only three sites were fished, Big Bay, Hay Bay, and Conway. The experimental gill net consisted of 45.7 m of each of 3.8- through 11.4-cm mesh (stretched measure) in 1.3-cm increments. This net was set overnight at each location. When smaller mesh sizes became excessively laden with alewife, the lengths of the 3.8-, 5.1-, and 6.4-cm mesh portions were reduced from 45.7 to 22.8 m. Nets were set parallel to the shore on the bottom at depths from 4 m in the upper bay to 12 m in the lower bay at Indian Point.

The catch per unit of effort (CUE) for gillnet catches was calculated on the basis of data adjusted to the catch from an overnight set of 91.4 m for each mesh size.

Trap net

During July of several years between 1969 and 1982, two 1.8-m trap nets with 3.8-cm mesh (stretched measure) were fished overnight for a period of six or seven nights. Two locations were chosen for these surveys: one in the upper bay near Trenton and the other in Hay Bay. The nets were positioned so the main trap was in about 3 m of water depth, and the 30.5-m leader was tied to shore. The unit of fishing effort for this gear was one overnight set.

Catch Processing

The total catch from each gear was counted by species and the total weight of each species was recorded. A subsample of 20–30 fish from each species was selected as randomly as possible. In the case of gillnet catches, a subsample was obtained from each mesh size fished.

The fork length and weight of each fish in the subsample were recorded, a scale sample or suitable bony segment (for aging) was obtained, the sex and state of maturity of the gonads were noted, and in some cases, the stomach contents were preserved.

Measure of Diversity

The diversity was measured by the Shannon Index (Shannon and Weaver 1949) at three sites representing the upper, middle, and lower bay from the combined May–August gillnet sets for each year.

The index of diversity is measured by (Clifford and Stephenson 1975)

$$(1) \qquad H' = \ln N - \frac{1}{N} \sum_{1}^{S} n \ln n$$

where H' is the diversity per individual specimen, N is the grand total of individuals of all species at one site, S is the number of species, n is the number of individuals of a given species.

Calculation of Evenness

The measure of the degree of equitability of individuals among the species in a community is termed evenness, and diversity is a measure that confounds both the number of species and their evenness in a collection (Pielou 1977). Pielou (1977) cautioned against the measure of evenness in situations where the number of species is unknown. It is assumed in the case of gillnet catches in the bay that species number and their relative abundance were known through the extensive sampling effort. In addition, it is assumed that sample removal did not significantly affect the total population. Christie and Scott (1985) discussed these same assumptions in regard to trapnet catches.

The equation to calculate evenness is as follows:

$$(2) \qquad V' = \frac{H'}{\log S}$$

where V' is evenness of the fish community and the other constants are as defined above.

Results and Discussion

Relative Abundance and Distribution of Fish

The Bay of Quinte supports a diverse fish fauna. Of 142 species of freshwater fish in the Atlantic Drainage Basin (Scott and Crossman 1973), 65 species representing 45 genera and 23 families inhabit this bay (Table 1). Most are generally associated with warm water, but a few cold-water forms are present for at least part of the year. Among the cold-water species are five salmonines that were recently introduced (or reintroduced) by man.

The discussion that follows is based on the experimental catches during 1969–83 with mention of catches made in Hay Bay beginning in 1958. Those species that comprise significant biomasses are discussed, while those that were taken in small numbers are simply listed in Table 1. In addition, several species were noted in Dymond et al. (1929) from collections made in 1928 but were not found in recent collections. These species are noted in Table 1.

Amiidae

Based upon gillnet catches, bowfin reached peak abundance in 1975–77 (Table 2). They were always most abundant in the upper bay, present in the middle bay, and rare in the lower bay. Bottom trawls rarely took bowfins, but trap nets routinely captured a few.

Clupeidae

Alewives, one of the two clupeids in our samples, were the most abundant species in the bay, as determined by both gill nets and trawls (Tables 2 and 3). Trap nets also captured large numbers of alewife at all sites. Beach seines, however, rarely took alewife.

Gillnet catches showed that alewife abundance at Hay Bay increased by a factor of 3 between the 1960s and the mid-1970s (Fig. 2). By the late 1970s they had decreased to levels prior to the 1970s. Between 1972 and 1976, alewife were more abundant in the upper bay than they were at Hay Bay. In 1977, however, alewife numbers were reduced in the upper bay, less so in the middle bay, and not in the lower bay (Table 2). Alewife numbers increased markedly in the lower bay between 1981 and 1983 but less so in the middle and upper bay. Predation by large numbers of walleye in the upper bay in 1977, and later years, probably reduced alewife numbers substantially (Hurley 1986a).

Trawl catches of alewife tend to reflect the gillnet catches, but are more variable largely because of the vulnerability of young-of-the-year (YOY) to trawls. For example, the biomass in the upper bay shifted in August to smaller weight classes when YOY alewife became vulnerable to the gear (Table 4). In the lower bay, adults were present in May, along with subadults, but less so from June onwards, reflecting their migration to the upper bay.

Trapnet catches of alewife showed a pattern of seasonal and site variations that was similar to those noted in gillnet and trawl catches. Trap nets set in the upper bay (Trenton–Deseronto) captured 89.6% of the alewife taken at all locations between Trenton and Allen Point (Fig. 1). During June and July, alewives moved closer to shore at the time of their spawning migration, and between 84.3 and 96.7% of the total catch was recorded at that time. Alewives were never very abundant in trapnet catches from the lower bay, during these months, probably due to their migrations into the upper bay.

The second of the clupeids in the bay, the gizzard shad, was always present in both gill nets and trawls in the upper bay (Tables 2 and 3). Fewer were taken in both the middle and lower bay. Adults were taken in greatest number in gill nets in June, July, and August, while YOY were taken in trawls in the upper bay from late July and peaked in August.

At Hay Bay from 1958 to the late 1960s, gizzard shad were a minor component of the catch but during the early 1970s they increased greatly in number. After the mid-1970s their numbers stabilized, but in the early 1980s they began to decrease substantially (Table 2).

Salmonidae

Two coregonines, lake herring and lake whitefish, in years up to the 1940s for lake herring and to the 1960s for lake whitefish, entered the bay each fall in large numbers to spawn (Christie 1973). A combination of predation by rainbow smelt on lake herring, increased eutrophication in the case of lake whitefish, and exploitation by an intense commercial fishery collapsed these stocks.

Both coregonines are still present in the bay and recent observations show a modest resurgence of lake whitefish. These fish originated from the small residual stock of lake whitefish that persisted in the less eutrophied areas of the lower Trent River. There is evidence that lake whitefish originating from open Lake Ontario are also augmenting the bay stocks.

Of the current salmonines in the bay, natural reproduction in rainbow trout and brown trout now enhances the population that

TABLE 1. Fish species found in the Bay of Quinte. Those species followed by D were recorded by Dymond et al. (1929) in 1928, but not in recent collections.

- Petromyzontidae - lampreys
  - *Petromyzon marinus* Linnaeus - sea lamprey
- Acipenseridae - sturgeons
  - *Acipenser fulvescens* Rafinesque - lake sturgeon
- Lepisosteidae - gars
  - *Lepisosteus osseus* (Linnaeus) - longnose gar
- Amiidae - bowfins
  - *Amia calva* Linnaeus - bowfin
- Clupeidae - herrings
  - *Alosa pseudoharengus* (Wilson) - alewife
  - *Dorosoma cepedianum* (Lesueur) - gizzard shad
- Salmonidae - whitefishes, ciscoes, salmons, and trouts
  - *Oncorhynchus kisutch* (Walbaum) - coho salmon
  - *Oncorhynchus tshawytscha* (Walbaum) - chinook salmon
  - *Salmo gairdneri* Richardson - rainbow trout
  - *Salmo trutta* Linnaeus - brown trout
  - *Salvelinus namaycush* (Walbaum) - lake trout
  - *Salvelinus fontinalis* (Mitchill) × *Salvelinus namaycush* (Walbaum) - splake
  - *Coregonus artedii* Lesueur - cisco, lake herring
  - *Coregonus clupeaformis* (Mitchill) - lake whitefish
  - *Prosopium cylindracum* (Pallas) - round whitefish (D)
- Osmeridae - smelts
  - *Osmerus mordax* (Mitchill) - rainbow smelt
- Hiodontidae - mooneyes
  - *Hiodon tergisus* Lesueur - mooneye
- Umbridae - mudminnows
  - *Umbra limi* (Kirtland) - central mudminnow (D)
- Esocidae - pikes
  - *Esox americanus vermiculatus* Lesueur - grass pickerel
  - *Esox lucius* Linnaeus - northern pike
  - *Esox masquinongy* Mitchill - muskellunge
- Cyprinidae - minnows and carps
  - *Carassius auratus* (Linnaeus) - goldfish
  - *Cyprinus carpio* Linnaeus - carp
  - *Notemigonus crysoleucas* (Mitchill) - golden shiner
  - *Notropis atherinoides* Rafinesque - emerald shiner
  - *Notropis chrysocephalus* (Rafinesque)[a] - striped shiner
  - *Notropis hudsonius* (Clinton) - spottail shiner
  - *Notropis spilopterus* (Cope) - spotfin shiner
  - *Notropis heterodon* (Cope) - blackchin shiner
  - *Notropis cornutus* (Mitchill) - common shiner
  - *Notropis bifrenatus* (Cope) - bridle shiner (D)
  - *Notropis stramineus* (Cope) - sand shiner
  - *Pimephales promelas* Rafinesque - fathead minnow
  - *Pimephales notatus* (Rafinesque) - bluntnose minnow
  - *Semotilus corporalis* (Mitchill) - fallfish
  - *Rhinichthys cataractae* (Valenciennes) - longnose dace
- Catostomidae - suckers
  - *Carpiodes cyprinus* (Lesueur) - quillback
  - *Catostomus commersoni* (Lacépède) - white sucker
  - *Hypentelium nigricans* (Lesueur) - northern hog sucker
  - *Ictiobus cyprinellus* (Valenciennes) - bigmouth buffalo
  - *Moxostoma anisurum* (Rafinesque) - silver redhorse
  - *Moxostoma macrolepidotum* (Lesueur) - shorthead redhorse
  - *Moxostoma valenciennesi* Jordon - greater redhorse
- Ictaluridae - bullhead catfishes
  - *Ictalurus nebulosus* (Lesueur) - brown bullhead
  - *Ictalurus punctatus* (Rafinesque) - channel catfish
  - *Noturus flavus* Rafinesque - stonecat
  - *Noturus gyrinus* (Mitchill) - tadpole madtom (D)
- Anguillidae - freshwater eels
  - *Anguilla rostrata* (Lesueur) - American eel
- Cyprinodontidae - killifishes
  - *Fundulus diaphanus* (Lesueur) - banded killifish

TABLE 1. (*Continued*)

- Gadidae - cods
  - *Lota lota* (Linnaeus) - burbot
- Atherinidae - silversides
  - *Labidesthes sicculus* (Cope) - brook silverside
- Gasterosteidae - sticklebacks
  - *Gasterosteus aculeatus* Linnaeus - threespine stickleback
  - *Culaea inconstans* (Kirtland) - brook stickleback
  - *Pungitius pungitius* (Linnaeus) - ninespine stickleback (D)
- Percopsidae - trout-perches
  - *Percopsis omiscomaycus* (Walbaum) - trout-perch
- Percichthyidae - temperate basses
  - *Morone americana* (Gmelin) - white perch
  - *Morone chrysops* (Rafinesque) - white bass
- Centrarchidae - sunfishes
  - *Ambloplites rupestris* (Rafinesque) - rock bass
  - *Lepomis gibbosus* (Linnaeus) - pumpkinseed
  - *Lepomis macrochirus* Rafinesque - bluegill
  - *Micropterus dolomieui* Lacépède - smallmouth bass
  - *Micropterus salmoides* (Lacépède) - largemouth bass
  - *Pomoxis nigromaculatus* (Lesueur) - black crappie
- Percidae - perches
  - *Etheostoma nigrum* Rafinesque - johnny darter
  - *Etheostoma flabellare* Rafinesque - fantail darter
  - *Perca flavescens* (Mitchill) - yellow perch
  - *Percina caprodes* (Rafinesque) - logperch
  - *Stizostedion vitreum vitreum* (Mitchill) - walleye
  - *Stizostedion vitreum glaucum* Hubbs - blue pike[b]
  - *Stizostedion canadense* (Smith) - sauger (D)
- Sciaenidae - drums or croakers
  - *Aplodinotus grunniens* Rafinesque - freshwater drum
- Cottidae - sculpins
  - *Cottus bairdi* Girard - mottled sculpin
  - *Cottus cognatus* Richardson - slimy sculpin (D)

[a] E.J. Crossman (Royal Ontario Museum, Toronto, Ont., pers. comm.) suggested that this form is different from *N. cornutus* in these collections.

[b] Now extinct in Lake Ontario (Crossman and Van Meter 1979).

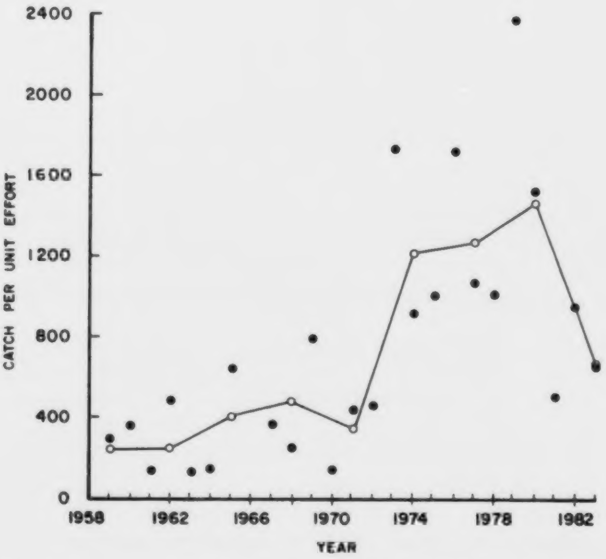

FIG. 2. Catch per unit gillnet effort for alewife at Hay Bay; ●, annual means; ○, means for 3-yr periods.

TABLE 2. Mean annual catch per unit of effort for standard experimental gillnet lifts from the upper, middle, and lower sections (UB, MB, and LB, respectively) of the Bay of Quinte

Species	Location	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Bowfin	UB	2.8	2.8	6.7	10.5	5.3	11.8	1.3	2.3	4.8	1.0	0.5	0.5
	MB	0.5	0.5	1.0	5.8	1.5	1.8	1.0	0.5	1.0	0	0	0
	LB	0.5	0.3	0	0.5	0	0.3	0	0.1	0	0	0	0
Alewife	UB	2019.2	3029.5	3872.5	2507.5	3110.5	348.5	923.7	1148.8	1004.7	311.0	558.0	1138.0
	MB	1176.8	2508.8	1099.5	1111.8	2872.5	1237.3	1224.8	2249.5	1368.0	512.0	925.5	639.0
	LB	376.3	2985.5	1124.8	818.5	1585.8	1229.8	2175.5	1630.8	2711.1	2561.5	2659.5	5337.5
Gizzard shad	UB	22.7	42.2	65.8	373.5	235.8	254.7	205.3	172.3	130.5	109.0	15.0	8.0
	MB	13.8	69.0	8.0	58.5	16.5	117.5	176.0	88.5	70.0	32.0	0	1.0
	LB	28.3	5.3	22.3	75.3	21.8	88.8	68.1	30.5	20.5	3.0	0.5	0
Rainbow smelt	UB	0.7	0	0	0.7	1.8	0	3.5	0	0	0	0	0
	MB	0.5	2.5	2.8	2.3	2.0	16.5	13.5	0.5	0.5	1.0	1.5	0.5
	LB	23.5	81.3	6.8	18.1	3.0	12.3	21.0	11.4	8.0	27.5	5.0	0
White sucker	UB	17.3	26.3	17.0	13.3	20.3	24.3	28.3	23.0	40.3	27.5	27.0	46.5
	MB	8.0	4.5	5.8	7.5	10.5	20.3	11.3	12.0	37.3	15.0	27.5	28.0
	LB	2.8	4.0	1.5	4.5	3.0	2.4	0.9	1.4	16.6	29.0	29.0	30.5
Brown bullhead	UB	23.5	45.5	90.7	89.8	81.0	111.2	116.2	64.8	88.0	47.0	40.0	16.5
	MB	18.5	25.0	22.3	98.8	56.3	155.8	71.3	22.8	39.3	21.5	1.5	2.5
	LB	5.0	0.8	2.8	2.1	0.5	1.1	0.9	0.1	0.3	0	0	0
Channel catfish	UB	5.8	6.5	18.3	4.2	3.8	4.3	14.0	17.2	21.7	14.0	7.5	13.5
	MB	1.0	0.3	0	0.5	0.5	0.5	4.5	5.0	1.5	1.0	0	0
	LB	0	0	0	0	0	0	0	0.1	0	0	0	0
White perch	UB	1000.2	995.8	1501.2	807.3	792.7	1086.0	142.0	266.7	447.0	679.5	556.5	383.0
	MB	879.8	700.5	566.3	674.3	508.8	949.5	168.8	135.3	149.8	119.5	6.0	40.5
	LB	348.0	305.0	343.0	330.4	335.6	314.6	39.9	44.6	52.1	28.0	9.5	43.5
Smallmouth bass	UB	3.2	4.7	8.0	5.5	8.5	8.3	19.2	21.8	22.3	15.5	31.0	23.0
	MB	2.8	2.3	0.5	1.3	0.5	9.3	9.8	4.5	3.5	7.0	3.0	0.5
	LB	0	1.0	0	3.5	0.6	1.1	2.3	2.0	1.0	0	0	1.0
Other centrarchids	UB	2.2	0.9	2.0	1.1	1.3	2.5	15.8	6.8	10.2	2.0	3.5	2.0
	MB	1.3	1.3	0.8	1.5	0.8	1.6	2.1	1.6	2.3	0	0	0
	LB	32.1	16.1	9.1	22.9	10.7	14.9	21.7	13.6	8.1	14.5	21.5	34.5
Yellow perch	UB	277.7	238.7	340.8	189.3	367.5	333.0	829.5	643.8	580.3	449.5	146.0	219.0
	MB	394.5	252.3	186.8	294.0	307.0	319.5	681.0	550.5	652.5	603.0	464.0	519.0
	LB	436.8	415.8	470.0	669.8	454.9	479.8	965.5	790.4	892.1	921.5	1337.5	573.5
Walleye	UB	1.3	1.8	4.0	2.3	3.7	3.0	25.2	32.3	65.8	163.5	109.5	47.0
	MB	2.5	3.0	1.0	1.0	0.8	1.3	14.0	17.5	87.5	32.5	0.5	0.5
	LB	0	0	0	0	0	0.1	2.0	34.0	21.0	3.5	0	15.5

was initially dependent on hatchery stocking. Current management initiatives have resulted in plantings of lake trout, coho and chinook salmon, and, to a lesser degree, splake. Natural reproduction within these species has not yet been demonstrated.

Osmeridae

Rainbow smelt were abundant only in the middle and lower bay. Gill nets took adults in May and June in the lower bay, and in recent years their numbers have decreased (Table 2). Trawls, however, took large numbers of YOY or yearling rainbow smelt especially in the lower bay in latter years (Table 3). YOY were most common in August and September, while yearlings were taken in May and June.

Esocidae

Among the esocids, only the northern pike were present in the bay in any number. Gillnet catches in the upper bay show a gradual increase since 1972, but year-to-year variability has been relatively large. The middle bay also produced comparable numbers of northern pike, but there is no evidence of any increase in numbers. The lower bay produced few northern pike, and numbers have fallen since 1978. Both grass pickerel and muskellunge occur within the bay, but were not taken in the test netting.

Cyprinidae

Fifteen species of this family were found in the bay (Table 1). Most of the species were taken in nearshore seine hauls, but carp, golden shiner, and spottail shiner were commonly present in both gill nets and bottom trawls. Carp, because of their large size, formed much of the biomass in the catch, particularly in the upper and middle sections of the bay. A few individuals were taken also in the lower bay.

Spottail shiners were taken in trawl drags in all areas and in all years (Table 3), and were also common in seine drags (Table 5). Although their numbers were variable over the years, there was a definite increase in all areas in 1983 (Table 3). Other cyprinids were less abundant in seine hauls, but since the nearshore community was not sampled as extensively as the offshore community, levels of abundance of some species may not be truly represented.

Catostomidae

Seven sucker species have been found in the bay, but only the

TABLE 3. Mean annual catch per unit of effort for standard bottom trawl drags from the upper, middle, and lower sections (UB, MB, and LB, respectively) of the Bay of Quinte. No fishing was done in 1982.

Species	Location	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1983
Alewife	UB	284.1	286.7	482.2	362.7	614.9	184.9	22.0	949.8	249.6	1158.9	265.0
	MB	379.6	615.7	563.8	229.4	922.6	46.9	83.7	479.3	97.8	340.5	100.4
	LB	353.8	222.1	1374.6	443.6	1493.6	182.9	168.9	31.3	39.1	1471.4	1469.4
Gizzard shad	UB	6.4	3.9	1.8	169.5	2.5	298.7	14.3	117.9	71.3	60.3	64.0
	MB	0	6.5	0.4	85.8	0.7	9.3	8.2	8.0	7.4	39.2	4.8
	LB	0.5	0.4	0.9	3.6	0	0.2	0	0	0.1	0	0.8
Rainbow smelt	UB	7.3	1.4	4.6	1.5	5.7	11.9	0.2	5.3	3.1	1.2	0
	MB	394.3	69.2	847.3	206.3	100.4	355.6	189.3	9.0	27.1	237.9	13.4
	LB	486.4	137.5	169.4	830.0	411.4	593.2	668.3	373.0	281.7	1335.5	2399.6
Spottail shiner	UB	4.8	1.6	0.6	1.7	0.7	0.2	1.2	0.4	5.7	0.3	4.0
	MB	15.9	5.5	4.2	2.7	4.0	4.0	41.0	7.5	0.1	0.8	19.6
	LB	0.4	0.3	0.1	7.3	57.7	1.5	7.3	1.2	0.2	5.9	33.0
Brown bullhead	UB	9.3	16.3	10.1	36.7	18.4	7.3	1.6	6.6	2.0	12.2	1.4
	MB	4.6	14.0	6.0	43.4	23.6	10.5	2.0	0.6	0.3	9.7	0.8
	LB	0	0	0	0.3	0	0.1	0	0	0	0	0
American eel	UB	6.3	6.8	3.1	4.1	4.3	4.6	0.9	4.1	0.5	4.3	1.2
	MB	6.0	2.6	4.3	7.3	4.6	2.0	0.9	0.6	0.6	3.7	1.0
	LB	0.2	0.2	0	0.3	0.1	0.1	0.1	0	0	0	0.2
Trout-perch	UB	23.3	14.9	7.9	12.4	45.1	1.2	1.3	1.5	0.8	5.6	9.4
	MB	5.3	7.1	2.0	2.0	4.7	1.3	2.5	1.8	0.6	16.4	70.4
	LB	21.0	18.7	19.7	131.2	195.7	11.3	51.7	5.5	4.6	37.0	226.0
White perch	UB	286.4	297.0	169.9	1061.8	270.0	539.4	1.5	92.3	66.3	721.8	103.6
	MB	478.6	452.9	240.9	461.8	718.7	335.0	4.0	30.3	35.1	194.6	14.2
	LB	386.5	781.0	92.9	155.3	314.3	25.7	0.8	0.3	2.3	29.0	8.6
Yellow perch	UB	59.5	17.7	6.1	20.8	35.6	34.8	1557.1	130.5	20.3	90.7	23.6
	MB	22.8	19.7	17.4	18.4	7.0	16.6	32.5	12.2	2.5	170.1	141.0
	LB	13.4	11.8	13.3	20.3	11.9	0.6	0.9	1.2	0.8	109.1	60.4
Walleye	UB	0.3	0	0.1	0.2	0.1	0.6	27.7	8.5	0.5	7.0	7.4
	MB	0.2	0	0	0	0.1	0	8.7	6.7	2.4	5.5	17.0
	LB	0	0	0	0	0.1	0	0.1	0.8	0.1	0.2	6.2

TABLE 4. Monthly estimated biomass (kg. $\cdot$ ha^{-1}) of alewife of different weight classes in two areas of the Bay of Quinte in 1981.

	Weight class (g)			
	0-3.1	3.2-9.9	10.0-31.5	31.6-99.9
Big Bay				
May	0	0	0	0
June	0	0	7.76	18.32
July	0.85	0	2.19	11.42
August	28.02	51.81	0	0
September	2.68	3.08	0	0
Conway				
May	1.46	48.84	64.48	426.73
June	0.18	10.24	16.73	22.78
July	0	0	50.40	56.57
August	0	0	0.87	1.95
September	0.09	1.43	0.19	0

TABLE 5. Catch per unit of effort for cyprinids from nearshore beach seines in the Bay of Quinte.

Cyprinid species	1980	1981	1982
Spottail shiner	19.1	10.1	7.2
Spotfin shiner	0.3	3.4	0
Bluntnose minnow	0.3	8.5	1.8
Fathead minnow	0.9	0.2	0
Blackchin shiner	0	0.2	0
Golden shiner	0	0.6	0
Carp	0	0.1	0
Emerald shiner	0	0.1	0
Sand shiner	0	0	0.2
Longnose dace	0	0	0.2

white sucker was present in appreciable numbers. Gillnet catches indicate that white suckers have increased in number since the late 1970s (Table 2). Over the longer term, data from the Hay Bay sets show a recovery in white suckers since the low period in the mid-1960s and early 1970s, but the population has not yet returned to the level seen there in the late 1950s and early 1960s. YOY white suckers were taken in late June (36–42 mm) and late July (58–65 mm) with beach seines in the middle bay.

A few specimens of *Moxostoma* were taken by trap nets set near Trenton. Northern hog suckers were taken in small numbers by gill nets under the ice in Hay Bay, and this appears to be an eastward extension of their range from the Humber River in Lake Ontario (Scott and Crossman 1973). A few specimens of quillback were also taken in the bay, but these are apparently absent from Lake Ontario (Scott and Crossman 1973). One specimen of bigmouth buffalo was taken near Glenora in 1981, and proved to be the first record of this species for Lake Ontario.

Ictaluridae

Among the three ictalurids found in the bay, brown bullhead and channel catfish were largely restricted to the upper and middle areas of the bay (Table 2). Stonecats were infrequently

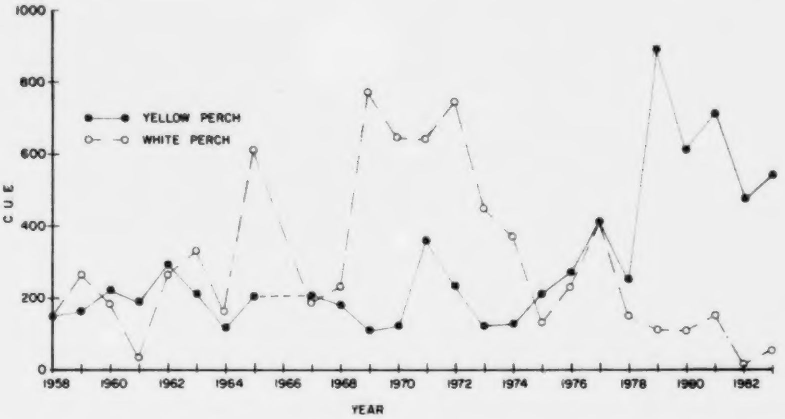

FIG. 3. Mean annual catch per unit gillnet effort values for white perch (○) and yellow perch (●) at Hay Bay, 1958–83.

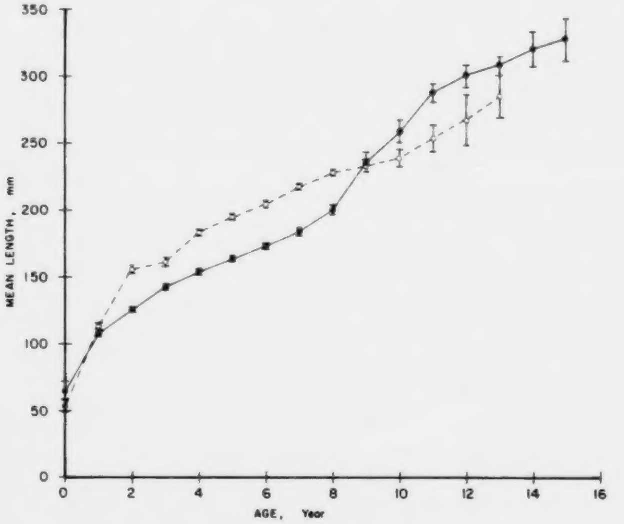

FIG. 4. Mean lengths (± 2 SE) at age of white perch taken in experimental gillnet sets in the Bay of Quinte in 1972–77 (●) and 1978–83 (○).

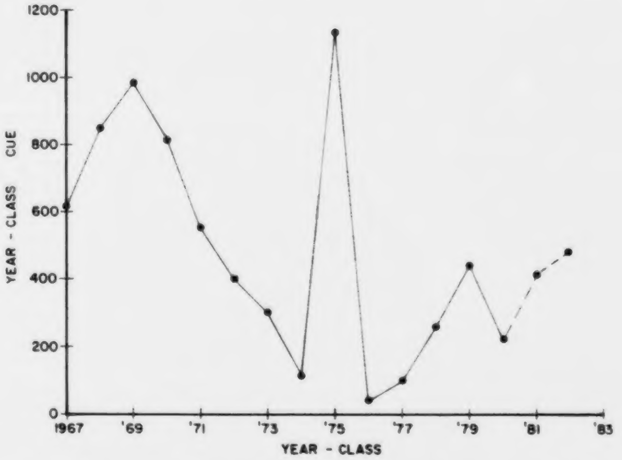

FIG. 5. Calculated year-class CUE for white perch year-classes from 1967 to 1982 based on gillnet catches. Broken lines indicate estimates based on less than 50% age class representation.

captured in gill nets set in deeper water at Indian Point and Lennox in the lower bay (Fig. 1).

Gillnet catches of brown bullhead increased during the 1972–77 period but fell below the 1972 level, after 1978. Trawl catches appear to follow the same trend but the maximum catches occurred in 1975 (Table 3). The average size of these fish taken in the trawls was smaller than from gill nets. Trapnet catches of brown bullhead were highest in the 1969–71 and 1981 periods and lowest in 1978 and 1979. Channel catfish were taken in relatively large numbers by trap nets in the upper bay.

Anguillidae

American eels were retrieved from almost every trawl drag in the upper and middle bay, but few were evident in the lower bay (Table 3). They were not vulnerable to the gill nets but were vulnerable to trap nets.

Percopsidae

Trout-perch were present in bottom trawls from all areas of the bay, but reached high numbers only in the lower bay (Table 3). It appears that the population declined drastically in 1977, after reaching a peak in 1976. Large numbers were again seen in 1983, particularly in the lower bay. This species was only infrequently present in gill nets and was not taken in trap nets or in nearshore seine hauls.

Percichthyidae

Next to alewife, white perch was the most common species found in the bay. They were taken in large numbers in all gears fished. White bass, although never present in large numbers, were taken at all locations in most years.

The rise of white perch in the Bay of Quinte, since their invasion from the Hudson River–Erie Canal route in the 1950s, has been decribed by Scott and Christie (1963) and Hurley and Christie (1977). Trends are characterized by catches at Hay Bay since 1958 (Fig. 3). There was a fairly steady increase up to the early 1970s but there followed an equally steady decrease after 1972. It is evident that some change had occurred in the bay during the early 1970s that halted the rise in numbers of white perch. In 1978 a virtual collapse of the white perch occurred

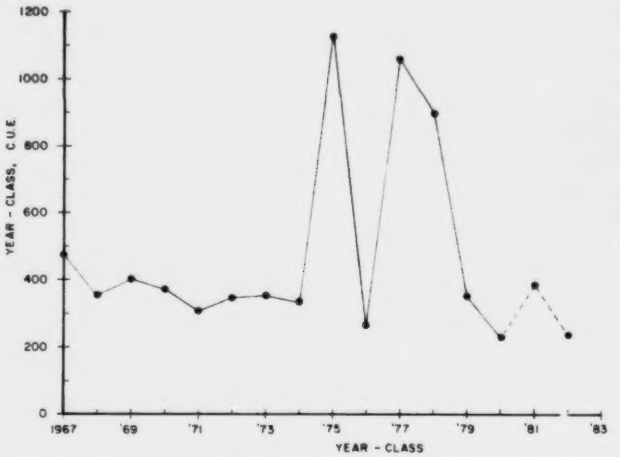

FIG. 6. Calculated year-class CUE for yellow perch year-classes from 1967 to 1982 based on gillnet catches. Broken lines indicate estimates based on less than 50% age-class representation.

(Tables 2 and 3). Some recovery was noted in the following years up to 1981 in the upper bay, but in 1982 and 1983, abundance in gill nets at all sites was again reduced. Similarly, bottom trawl catches rose sharply in 1981, but fell again in 1983.

The growth rate of white perch in the period 1957–66 in the Bay of Quinte was inversely related to population density (Sheri and Power 1972). Data from the 1972–83 period show a similar phenomenon. The mean length of gillnet-caught white perch in the 1978–83 period showed an increase in growth of age 2–8 fish. This occurred after the large reduction in the white perch population in early 1978 (Fig. 4). The mean lengths at each age for the two groups from 2 through 8 are significantly different. However, the length–weight regressions for the two periods were not significantly different (F (coefficient) = 0.18, df = 1, 26; F (elevation) = 0.16, df = 1, 27).

Among the 1972–77 group, a discontinuity in the growth rate was evident in ages 9 and older (Fig. 4). This may result from an increased survival of larger members of these age groups, or from remaining members of the faster growing individuals from the early 1960s. Similarly, older white perch (age 9 and over) in the 1978–83 group would include members of the slower growing 1972–77 cohorts and thus cause the slight reduction in length-at-age noted in the 1978–83 group.

The gillnet CUE values for ages 1 and older were summed for individual year-classes from 1967 to 1978 to obtain values for year-class strength. Data for years after 1978 did not include all age groups so that estimates for year-class strength for 1978 and later are tentative. Values for year-class strength reached a peak in the late 1960s, fell to a low point in 1974, rose sharply as the result of the large 1975 year-class, dropped to a low value in 1976, and rose slightly since then (Fig. 5). The rising trend in the CUE values for 1978 and 1979 year-classes reflects a higher production of young white perch, but their rate of survival may not be as great as it had been in the 1960s.

Centrarchidae

The centrarchids were well represented in all areas of the bay. Smallmouth bass were common in the upper bay and have shown a slow but steady increase in abundance since 1972 (Table 2). Among the other centrarchids, rock bass and pumpkinseed were most common in the lower bay (Table 2). Black crappie, largemouth bass, and bluegill were taken in small numbers at most locations.

Trapnet catches at Trenton have shown a significant increase in smallmouth bass since 1978. This increase was not paralleled in Hay Bay where it may reflect a poorer habitat. Rock bass abundance has increased in all locations, but especially in the lower bay during the 1972–83 period. Pumpkinseeds also have increased in the upper bay since the late 1960s, but have shown a decline at Hay Bay since then.

Percidae

The Bay of Quinte provides ideal habitat for percids, and four of the five species found in the area are common.

Yellow perch abundance, as measured by gill nets at Hay Bay, remained at a CUE of about 200 between 1958 and 1978 (Fig. 3). Since then, CUE has increased to about 700 (1979–83). The abundance of yellow perch increased markedly after the white perch collapsed in the late 1970s. However, the yellow perch did not decrease during the period in the 1960s and early 1970s when white perch abundance increased markedly (Fig. 3). Unlike white perch, the growth rate of yellow perch increased in the 1978–83 period as their abundance increased. Growth rates of yellow perch aged 2, 3 and 4 were not significantly reduced in the 1960s and early 1970s when white perch abundance increased. However, yellow perch aged 5 and older were between 10 and 25 mm shorter in the period when white perch were abundant. It appears, therefore, that some degree of interspecific competition may occur, although their diets showed significant overlap only in the lower Bay of Quinte (Hurley 1986b).

The increased yellow perch abundance in the late 1970s and early 1980s is directly related to the production of several strong year-classes beginning in 1975 and continuing in 1977 and 1978 (Fig. 6). Year-class strength after 1978 appears to be similar to that measured between 1967 and 1974. The data for the 1981 and 1982 year-classes are incomplete because not all age-classes are represented in the 1983 catches, and values assigned for these year-classes are tentative.

Trawl catches of yellow perch were generally low at all sites except in 1978 when large numbers of YOY were taken in the upper bay (Table 3). Abundance increased at most sites in 1978 and later years. This reflects the similar increases noted in gillnet catches.

Walleye play a pivotal role among fish species in the bay as the major fish predator in the community. Walleye abundance dropped sharply after the passage of the large 1959 year-class. But, there remained a residual stock within the bay that produced a sizeable year-class in 1977 and a very large one in 1978.

Gillnet catches from the upper, middle, and lower bay show low numbers of walleye through the early and middle 1970s and a dramatic increase that began in 1978 (Table 2).

Trawl catches similarly showed the presence of large numbers of walleye in 1978, especially in the upper bay (Table 3). Most of these were YOY or yearlings. Trawls were ineffective in capturing walleye greater than 300 mm in length. Trap nets caught few walleye in the 1969–71 period, but from 1978 on, at Trenton, their numbers increased. Trap nets caught few walleye in Hay Bay.

The long-term Hay Bay gillnet series was used to compare the recent upturn in walleye abundance with that recorded in the 1950s. Year-class CUE values were calculated from the age composition of the sampled fish. These values show large year-classes in 1955 and 1959 followed by a gradual reduction in year-class strength through 1976 (Fig. 7). The 1977 year-class

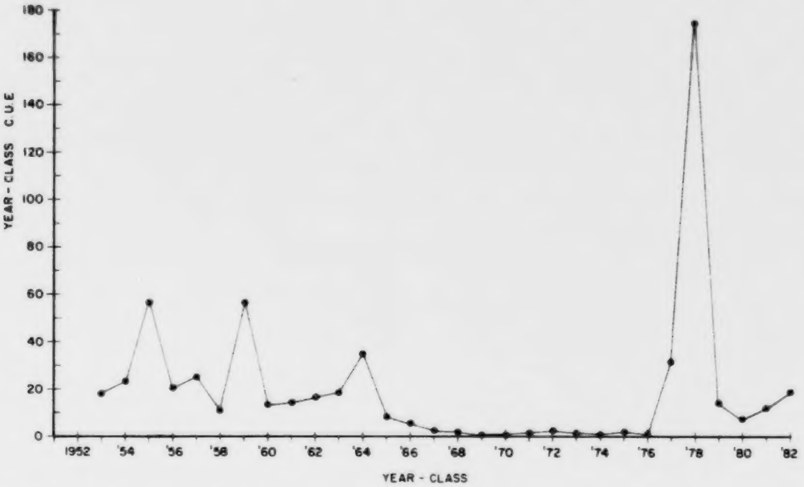

FIG. 7. Calculated year-class CUE for walleye year-classes from 1953 to 1982 based on gillnet catches. The value for 1982 is based on less than 50% age-class representation.

proved to be the largest since the late 1950s; this was followed by an extremely large year-class in 1978. Year-class strength for 1979 and later years appears to be approaching the level shown by the majority of year-classes in the 1953–64 period (Fig. 7).

Diversity of Fish Species

Diversity was calculated from the Shannon Index, H', at three sites in the bay. Diversity at Big Bay has increased fairly steadily from below 1.0 in 1972–73 to 1.3 and 1.7 in 1981 and 1983 (Fig. 8a). Values in the 1972–76 period, when nutrient concentrations were high (70–90 μg total phosphorus $\cdot$ L^{-1}), ranged between 0.94 and 1.2. Values in the 1978–83 period, when nutrient concentrations were substantially reduced (46–53 μg total phosphorus $\cdot$ L^{-1}), ranged between 1.3 and 1.7. In 1977, diversity was relatively high (1.5) even though total phosphorus concentration (70 μg $\cdot$ L^{-1}) was also high.

At Hay Bay, diversity has dropped fairly steadily since 1958, with recent values being particularly erratic (Fig. 8b). There appears to have been no upward trend in diversity in response to changing nutrient concentrations. However, values recorded between 1972 and 1983, which correspond to the period shown for Big Bay (Fig. 8a), exhibit extreme variability. Concentrations of total phosphorus in this period at Hay Bay ranged between 34 μg $\cdot$ L^{-1} (1979) and 63 μg $\cdot$ L^{-1} (1972).

The diversity indices for the Conway site have fallen steadily since 1975 (Fig. 8c), and are the reverse of the trend noted at Big Bay. Diversity at Conway tended to be generally the lowest of any of the three sites. Total phosphorus concentrations at Conway showed virtually no change throughout the 1972–83 period (18–24 μg $\cdot$ L^{-1}).

Species number in the upper bay varied between 13 and 21 with no apparently consistent trend (Fig. 8a). The rise in diversity, therefore, is related more to greater evenness in the collections than to a change in species composition. Values for evenness rose from an average of 0.87 in 1972–74, to 1.16 in 1977–79, to 1.26 in 1981–83. Much of this increased evenness is due to the reduction in the numbers of alewife and white perch and the rise in numbers of white sucker, smallmouth bass, and walleye.

In the middle bay, the number of species in the collections dropped steadily from the late 1950s to the 1970s and has not changed appreciably since then (Fig. 8b). For example, blue pike and northern hog sucker have not been taken since 1960 or earlier; burbot, spottail shiner, bluegill, and largemouth bass have not been taken at Hay Bay since the late 1960s. Species such as white bass, rock bass, pumpkinseed, smallmouth bass, and black crappie, which were regularly taken in small numbers in the early 1960s, tended to be sporadic in catches during the 1970s. The fall in diversity in this case results from the loss of several species in the collections. Evenness varied between 0.66 and 1.29 throughout the series from 1958 to 1983 with no obvious pattern.

The number of species taken and the diversity of the catch in the lower bay dropped between 1975 and 1983 (Fig. 8c). Evenness also fell in this same period from 0.98 in 1975–77 to a low of 0.47 in 1983. Alewives have increased greatly in abundance in the lower bay in the 1975–83 period, while the abundance of gizzard shad, white perch, and, to a lesser extent, rainbow smelt fell. These species shifts resulted in the observed changes in the calculated indices.

Factors Influencing Species Composition

The role of climate

Water temperature establishes the rate of physiological processes that determine the time of maturity and spawning as well as growth rate. For some species it also establishes the rate of survival through growth parameters (e.g. in smallmouth bass; MacLean et al. 1981) or the hatching success and early life history stages (as in the percids; Busch et al. 1975; Eshenroder 1977; Shuter et al. 1979).

An analysis of the spring temperature increase and walleye year-class strength was made for the Bay of Quinte. A regression was calculated between the rate of water warming (from date at 6°C to May 15) and year-class strength. The 6°C starting temperature was chosen because peak arrival of female walleye on the spawning grounds occurred at that temperature (J. Radford, LOFAU, R.R. 4, Picton, Ont. K0K 2T0, pers. comm.). Wolfert et al. (1975) observed that peak spawning of walleye occurred at 7°C in western Lake Erie. The mean rate of temperature increase from the date at which 6°C was reached until May 15 for the years 1953–82 was 0.253° per day with a standard deviation of 0.123. The distribution of the rates was approximately normal.

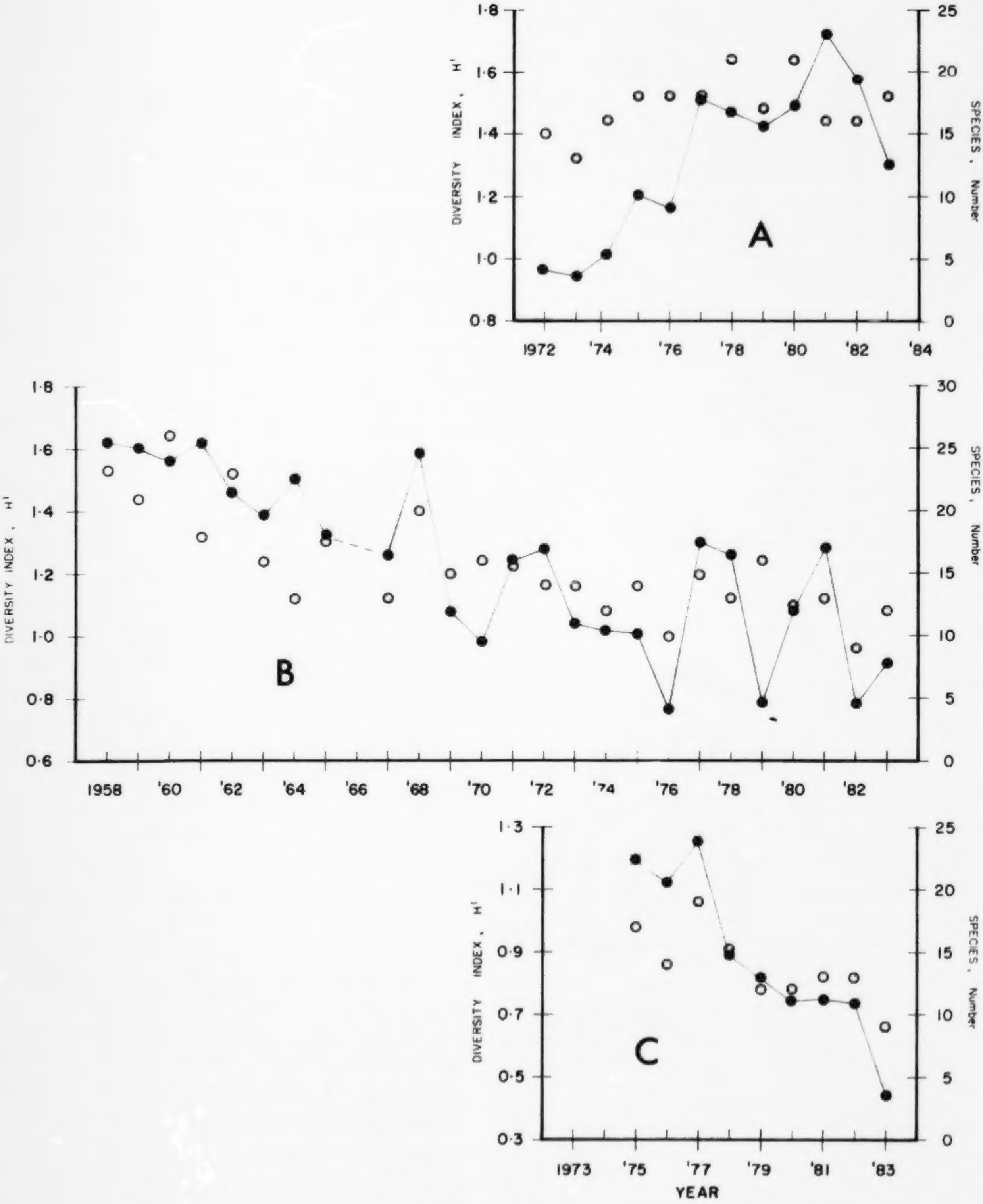

FIG. 8. Diversity indices (●) and species number (○) obtained from gillnet sets in the upper Bay of Quinte (A), the middle Bay of Quinte (B), and the lower Bay of Quinte (C).

It appears that factors other than the spring temperature rise have been responsible for the establishment of strong year-classes for yellow perch and walleye. The regression of walleye year-class strength on the rate of spring temperature increase was not significant ($R^2 = 5.0\%$). The most obvious disparity between the two measurements was the failure of year-classes in the 1965–76 period, when above-average spring temperature increases occurred in 5 of the 11 years. Data on year-class strength of yellow perch from 1967 to 1982 were also regressed on spring temperature rise, but again the regression was not significant ($R^2 = 2.9\%$). The apparent failure of year-classes in springs when the rate of warming was above average produced the poor correlation.

The stock-recruitment relationship among walleye in western Lake Erie, studied by Shuter et al. (1979), showed a positive effect of stock size on recruitment. No thorough analysis of the same relationships in the Bay of Quinte stock has been made. The production of the 1977 and 1978 year-classes, after the almost complete failure of the 1969–76 year-classes, indicates that the potential recruitment from relatively few spawners can be very large.

Forney (1971) cited predation as the primary regulator of yellow perch abundance in Oneida Lake. He did not mention spring temperatures, during incubation, as a factor in developing year-class strength. He did remark, however, that the size of larval yellow perch in mid- to late June and their growth rate might determine year-class strength.

There is no evidence that high water temperatures in the summer have had adverse effects on most of the fish populations in the bay. The range of means for June, July, and August water temperatures at Belleville for the years 1952–81 was 20.2 to 23.9 ± 1.7°C, and these temperatures are favourable for a warmwater fish community.

However, growth rates of adult walleye, predicted by a bioenergetics model, approached zero when water temperatures were in excess of 23.5°C (Hurley 1986a). Daily water temperatures recorded at the Belleville Filtration Plant were representative of the Bay of Quinte water temperatures from Trenton to Hay Bay from the end of May to the end of October (Hurley 1986a). Only once, in 1976, during the years 1972–83 did the summer water temperatures not exceed 23.5°C. In the remaining years, that temperature was exceeded an average of 37 d each year beginning as early as June 12 and as late as July 21. The range in the number of days when temperatures exceeded 23.5°C was from 6 in 1972 to 62 in 1983. The migration of a large proportion of adult walleye age 4 and older to Lake Ontario soon after spawning (Payne 1963) is probably a behavioural response to high summer water temperatures in the bay.

There is only one occasion in recent times when colder than normal winter water temperatures have adversely affected a fish population in the bay, and this occurred in the case of white perch in 1978. There are fisherman's reports that a massive die-off of white perch occurred overwinter in the lower bay in 1977–78 (R. McIntosh, Glenora Fisheries Station, R.R. 4, Picton, Ont. K0K 2T0, pers. comm.). Bottom trawl drags in the eastern basin of Lake Ontario retrieved large numbers of dead white perch during May and June of 1978. The winter of 1978 was severe in this area with very late spring warming, and there were large ice flows in Lake Ontario well into May, far later than usual.

The effect of extreme winter conditions in 1978 has been examined by using water temperatures in the January–April period. Based on Kingston water temperatures, which should closely match the regime of the lower bay where white perch congregate in winter, the mean water temperature for January–April for 1978 (0.95°C) was considerably below any other year during the 1970–82 period. The value falls well outside the 99% confidence interval (1.19–1.63°C). It is probable that the colder than normal March and April water temperatures caused the mass mortalities among white perch, which, in the Bay of Quinte, are at the northern edge of their freshwater distribution.

The role of eutrophication

Nutrient inputs affect fish populations primarily through change in the abundance of their food organisms. Algal density, increased by nutrient inputs, affects water clarity, zooplankton composition and biomass, macrophyte abundance, and, through biochemical degradation, oxygen concentrations near the bottom, and thereby composition of the benthic community. Hurley and Christie (1977) compared the Bay of Quinte with West Lake, a similar body of water that had not received large quantities of nutrients, and found that West Lake had a healthy stock of large piscivores, but the Bay of Quinte did not. They did not, however, demonstrate a direct impact of eutrophication on piscivores.

Fouling of spawning areas by the accumulation of dead and decaying algae has been cited as a reason for the decline of lake whitefish in the bay (Christie 1973). There can be little doubt that this was an important factor, and it is probably the best example of a direct effect of eutrophication. The fact that fishermen in the bay noted that gill nets became badly coated with dense algal mats in the 1950s is further indication of the degree of eutrophication in the bay.

The role of piscivores

The loss of large piscivores in the 1960s and early 1970s has been cited as the primary cause of the expansion of small-sized species in the bay (Hurley and Christie 1977). The interaction between piscivores and their prey was more fully examined by Christie and Scott (1985), but the trend to inverse abundances can be seen in Table 6. Trapnet catches of piscivores accounted for a generally smaller percentage of the fish biomass at both Trenton and Hay Bay in 1969–71 than in 1976 and later. Catches in 1978 do not conform to this observation, but piscivore abundance was low in that year at both sites.

Planktivore (mainly alewife) abundance was high in the 1969–71 period, but fell sharply when piscivores began to increase. Benthos feeders tended to vary throughout the series, but appear to be following a downward trend at Trenton in the years 1979, 1981, and 1982. The proportion of the white perch taken at Trenton that were sufficiently large to be piscivorous increased markedly from 1978 to 1982. This was the result of an increased growth rate after 1978. In 1979, 32% of the white perch were large enough to be piscivorous, 47% in 1981, and 89% were large enough in 1982. The data in Table 6 reflect this change in feeding habit among white perch. Similarly, among white perch in Hay Bay, 35% in 1979 and 63% in 1982 were large enough to be piscivorous.

Stomach contents of large piscivores in the 1977–81 post-phosphorus control period showed that alewife was the most common food item, with rainbow smelt, yellow perch, and white perch the next most common items (Table 7). Other fish species were also eaten by large piscivores, but their frequency of occurrence was usually less than 5%.

It appears that the recent increase in piscivores in the bay has resulted in a decrease in the abundance of small-sized prey together with an increased growth rate of five species of benthivores (Christie and Scott 1985). Larger sized fish, therefore, have become more prevalent than they were in the early

TABLE 6. Percentage of biomass of trapnet catches by major feeding types.

	Trenton						Hay Bay				
	1969–71	1976	1978	1979	1981	1982	1969–71	1976	1978	1979	1982
Biomass (kg · net night^{-1})	66.74	28.34	26.19	170.76	119.12	113.21	52.64	17.42	23.79	8.93	15.76
Piscivores	16.8	28.1	16.2	34.8	50.2	57.3	19.3	41.0	14.8	37.8	45.2
Planktivores	39.9	2.1	1.7	3.3	7.0	0.8	18.6	0.2	4.8	2.7	1.3
Herbivores	0	0.5	1.5	2.8	0.4	0	<0.1	3.8	6.7	7.2	0
Benthivores	43.3	69.4	80.7	59.1	42.4	41.9	62.0	55.0	73.7	52.3	53.5

TABLE 7. Stomach contents of large piscivores taken in experimental gill nets, May–August, in the Bay of Quinte, 1977–81, given as the percentage of occurrence.

Food item	Bowfin	Longnose gar	Northern pike	Channel catfish	Smallmouth bass	Walleye
No. of fish with food	54	45	88	191	170	589
Alewife	24.1	51.1	39.8	3.1	12.9	28.5
Rainbow smelt	3.7		8.0	0.5	6.5	15.6
Yellow perch	11.1	4.4	17.0		7.1	3.9
White perch	5.6		11.4			1.2
Brown bullhead	5.6					
Rock bass	1.9					
Johnny darter		4.4				0.7
Centrarchids			2.3		0.6	
Gizzard shad						0.7
Mottled sculpin						0.2
Threespine stickleback						0.2
Unidentified fish	61.1	44.4	30.7	28.8	54.1	53.0
Crayfish	3.7			1.0	18.2	
Chironomids				49.7	5.9	

1970s. This shift to a larger size within the fish community is a reversal of the trend of the 1960s and early 1970s.

The role of fisheries

The reported annual commercial harvest from the Bay of Quinte has averaged 390 000 kg in the period from 1956 to 1983. Significant changes in the composition of the harvest occurred when lake herring collapsed in the 1940s, possibly because of predation by and competition from rainbow smelt (Christie 1973). Lake whitefish collapsed in the 1960s because of year-class failures after 1957, possibly due to effects of eutrophication and the stress of exploitation rates of 50–65% (Christie 1973).

Commercial harvests of American eel and ictalurids have remained fairly constant over the years 1956–83. Harvest of white perch rose quickly as the population expanded to reach 130 000 kg annually in the mid-1970s, but the harvest fell dramatically when the population crashed after 1978. Landings of yellow perch have increased since the 1960s, while landings of walleye decreased, firstly because of the falling population, and latterly because of their removal from the list of commercial species after 1981. Restrictions on the sale of some species, such as American eel and carp, because of high contaminant levels have reduced the harvest of these species in some years.

The sport fishery in the Bay of Quinte was rejuvenated in the late 1970s when walleye abundance increased. Current estimates of the annual walleye harvest are 91 000 kg (Dentry 1985). Significant annual harvests of several other species from the sports fishery are recorded: northern pike, 12 000 kg; brown bullhead, 1400 kg; white perch, 20 000 kg; yellow perch, 40 000 kg. The total annual sport harvest for all species was 217 000 kg in 1984 (Dentry 1985).

In spite of the substantial harvest of fish of many species in the bay, there is no clear evidence that exploitation alone has ever resulted in a demonstrable decline in stocks (W.J. Christie, Glenora Fisheries Station, R.R. 4, Picton, Ont. K0K 2T0, pers. comm.). However, the combined effects of exploitation, eutrophication, introduction of non native species, and climatic shifts have resulted in dramatic reductions in certain fish stocks in the bay (Hurley and Christie 1977). Unfortunately, most of the declines occurred in the more commercially valuable species.

Fish Community Structure

Water quality in the Bay of Quinte passed through stages from mesotrophy to hypereutrophy in a period of about 30 yr from the 1940s to the 1970s. The upper, shallow sections of the bay were most affected, while the lower, deeper sections were least affected by increasing eutrophy. For many decades prior to the 1950s, the bay supported a community dominated by percids and also large numbers of coregonines. Lake herring and lake whitefish migrated to the bay and spawned, and the early life stages of these species remained in the bay. In addition, centrarchids, ictalurids, and osmerids were well represented in some sections of the bay. Clupeids entered the bay in spring and spawned, and the young spent their first year or so of life there. In the case of alewives and coregonines, biomass that had been developed from nutrients derived from Lake Ontario was transferred to the Bay of Quinte.

However, increased nutrient inputs during the 1950s as the result of increased detergent use and up to the mid-1970s as the result of population increases stressed the mesotrophic community, and it became more eutrophic. Many of the changes observed in the bay find their parallels in other water bodies

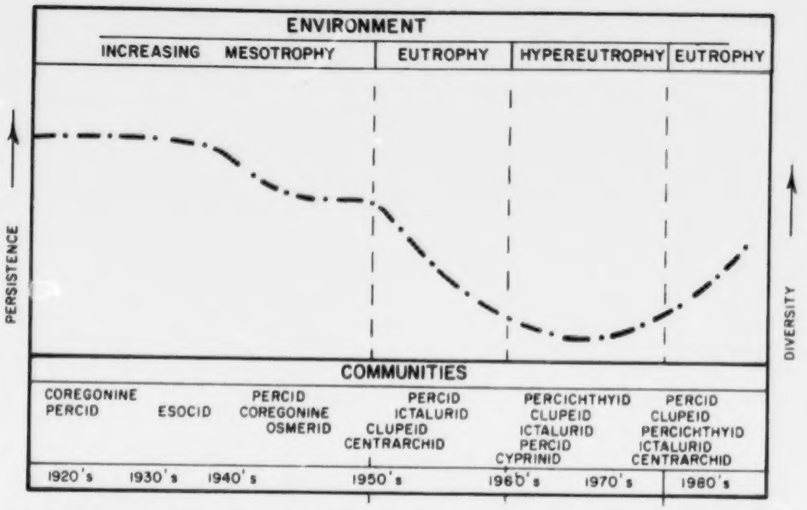

FIG. 9. Schematic representation of fish community changes seen in the Bay of Quinte from the 1920s to the present (adapted from Ryder and Kerr 1978).

which have been described by Leach et al. (1977).

First, the coregonines declined when lake herring largely disappeared by the mid-1940s probably as a result of predation on their young by osmerids (Christie 1973). Lake whitefish survived to the 1960s but succumbed to the effects of percichthyid predation and degraded conditions in the spawning grounds (Hurley and Christie 1977). Meanwhile, walleye increased in the 1940s and 1950s, but the population crashed in the 1960s possibly because of percichthyid predation. A percichthyid, the white perch, invaded the bay and proliferated in the 1960s and early 1970s. By the early 1970s the upper bay was dominated by clupeids and percichthyid, with ictalurids and catastomids persisting, but centrarchids reduced. A reduction in centrarchids was also noted by Christie and Scott (1985) in a lake where, simultaneously, white perch proliferated. Osmerids, however, maintained their numbers in the lower bay. One percid, yellow perch, persisted despite the pressure of the percichthyid. Throughout this time, small numbers of walleye continued to spawn in the rivers of the upper bay, but survival was thought to be poor. A few lake whitefish also persisted in the relatively mesotrophic waters of the Trent River, and some spawning occurred there.

A dramatic reversal of the trend towards extreme eutrophication occurred in the late 1970s and 1980s, with sharp reductions in phosphorus inputs. However, a significant part of the observed change in fish populations that occurred when eutrophication was halted was due to climatic extremes which resulted in cooler than normal temperatures in the winter of 1977–78. The numbers of white perch that died in this period must have been very large, judging from subsequent changes observed in gillnet and trawl catches. Concurrently in 1977, and especially in 1978, percid abundance rose dramatically. Centrarchids, particularly smallmouth bass, became more abundant after the mid-1970s, while clupeids declined. This return of centrarchids when white perch declined is further evidence of the reciprocal relationship between these species noted by Christie and Scott (1985). Recent evidence is also strong that lake whitefish are becoming more abundant in the lower bay, and small numbers of adults in spawning condition are now regularly taken in the upper bay in the fall. The presence of walleye from several year-classes points to a generalized improvement in their rate of survival.

Ryder and Kerr's (1978) schematic representation of fish communities of the boreal forest area can be modified to illustrate the situation in the Bay of Quinte (Fig. 9). Their salmonine community of the oligotrophic stage can be described as a mesotrophic, coregonine community for the bay, in which both species persistence and diversity are relatively high. The bay, because of its shallowness and relatively enriched state, was probably not oligotrophic, at least since 1900 (Warwick 1980). The shift from mesotrophy to eutrophy occurred in the 1960s, and to hypereutrophy in the 1970s. The later mesotrophic community in the bay in the 1940s and 1950s was a mixed percid–coregonine–esocid one with lesser numbers of osmerids, clupeids, ictalurids, and centrarchids. The hypereutrophic community was composed of dominant clupeid–percichthyid, with ictalurids and cyprinids playing a smaller role. Data from the long-term Hay Bay series show that while the diversity of the community decreased at each stage, the total biomass increased.

Reduction in nutrient inputs and the increased abundance of piscivores have resulted in the initiation, at least, of a process whereby the present community is beginning to resemble that seen in the late 1950s and early 1960s, where percids, clupeids, ictalurids, and centrarchids were major taxa. The recent increase in coregonines may herald the beginning of a return of this group to the position it held in the 1950s.

The persistence of a fish community resembling that of the 1950s will depend on the presence of significant numbers of piscivores which, in turn, appears to depend on some tolerable level of water quality. Although the exact nature of this level is not known, it appears to be close to that present in the late 1970s and early 1980s.

References

ANONYMOUS. 1981. Project Quinte Ninth Annual Report 1980. Glenora Fisheries Station, R.R. 4, Picton, Ont. K0K 2T0. 37 p.

BAUMANN, P.C., J.F. KITCHELL, J.J. MAGNUSON, AND T.B. KAYES. 1974. Lake Wingra, 1837–1973: A case history of human impact. Wis. Acad. Sci. Arts Lett. 62: 57–94.

BLAXTER, J.H.S., B.B. PARRISH, AND W. DICKSON. 1964. The importance of vision in fish reaction to drift net and trawls, p. 529. *In* Modern fishing gear of the world. Vol. 2. Second F.A.O. World Fishing Gear Congress, London, 1963.

Busch, W.-D. N., R.L. Scholl, and W.L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960–70. J. Fish. Res. Board Can. 32: 1733–1743.

Christie, W.J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23: 65 p.

Christie, W.J. and K.A. Scott. 1985. Rehabilitation prospects for the Bay of Quinte fish community after phosphate control. File Report, Glenora Fisheries Station, Picton, Ont. K0K 2T0.

Clifford, H.T., and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York, San Francisco, London.

Crossman, E.J., and H.D. Van Meter. 1979. Annotated list of the fishes of the Lake Ontario watershed. Great Lakes Fish. Comm. Tech. Rep. 36: 25 p.

Dentry, W. 1985. Projecting annual harvest by anglers in the Bay of Quinte. Lake Ontario Fisheries Assessment Unit, Internal Report LOA 85.9, R.R. 4, Picton, Ont. K0K 2T0.

Dymond, J.R., J.L. Hart, and A.L. Pritchard. 1929. The fishes of the Canadian waters of Lake Ontario. Publ. Ont. Fish. Res. Lab. No. 37.

Eshenroder, R.L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34: 1830–1838.

Forney, J.L. 1971. Development of dominant year classes in a yellow perch population. Trans. Am. Fish. Soc. 100: 739–749.

Hurley, D.A. 1986a. Growth, diet and food consumption of walleye (*Stizostedion vitreum vitreum*): an application of bioenergetics modelling to the Bay of Quinte, Lake Ontario, population, p. 224–236. *In* C.K. Minns, D.A. Hurley, and K.H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. Effect of nutrient reduction on the diets of four fish species in the Bay of Quinte, Lake Ontario, p. 237–246. *In* C.K. Minns, D.A. Hurley, and K.H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Hurley, D.A., and W.J. Christie. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Leach, J.H., M.G. Johnson, J.R.M. Kelso, J. Hartmann, W. Numann, and B. Entz. 1977. Responses of percid fishes and their habitats to eutrophication. J. Fish. Res. Board Can. 34: 1964–1971.

MacLean, J.A., B.J. Shuter, H.A. Regier, and J.C. MacLeod. 1981. Temperature and year-class strength of smallmouth bass. Rapp. P.-V Réun. Cons. Int. Explor. Mer. 1978: 30–40.

Minns, C.K., and D.A. Hurley. 1986. Population dynamics and production of white perch, *Morone americana*, in the Bay of Quinte, Lake Ontario, p. 215–223. *In* C.K. Minns, D.A. Hurley, and K.H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Payne, N.R. 1963. The life history of the yellow walleye, *Stizostedion vitreum* (Mitchill), in the Bay of Quinte. M.A. thesis, University of Toronto, Toronto, Ont.

Pielou, E.C. 1977. Mathematical ecology. John Wiley & Sons, New York, London, Sidney, Toronto.

Ryder, R.A., and S.R. Kerr. 1978. The adult walleye in the percid community — a niche definition based on feeding behaviour and food specificity. Am. Fish. Soc. Spec. Publ. 11: 39–51.

Scott, W.B., and W.J. Christie. 1963. The invasion of the lower Great Lakes by the white perch, *Roccus americanus* (Gmelin). J. Fish. Res. Board Can. 20: 1189–1195.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Shannon, C.E., and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, IL.

Sheri, A.N., and G. Power. 1972. Effect of density on the growth of white perch, *Roccus americanus* (Gmelin), in the Bay of Quinte, Lake Ontario. Pak. J. Zool. 4: 109–132.

Shuter, B.J., J.F. Koonce, and H.A. Regier. 1979. Modeling the western Lake Erie walleye population: a feasibility study. Technical Report, No. 32, Great Lakes Fishery Commission, Ann Arbor, MI.

Sly, P.G. 1986. Review of postglacial environmental changes and cultural impacts in the Bay of Quinte, p. 7–26. *In* C.K. Minns, D.A. Hurley, and K.H. Nicholls [ed.]. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Warwick, W.F. 1980. Palaeolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 117 p.

Wolfert, D.R., W.N. Busch, and C.T. Baker. 1975. Predation by fish on walleye eggs on a spawning reef in western Lake Erie 1969–71. Ohio J. Sci. 75: 118–125.

Population Dynamics and Production of White Perch, *Morone americana*, in the Bay of Quinte, Lake Ontario

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Minns, C. K., and D. A. Hurley. 1986. Population dynamics and production of white perch, *Morone americana,* in the Bay of Quinte, Lake Ontario, p. 215–223. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.]. Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

All available data on the 1950's invasion and proliferation of white perch (*Morone americana*) in the Bay of Quinte, a freshwater embayment of Lake Ontario, are analyzed and summarized. The life history parameters are shown to be similar to those for this species in its native habitat, Atlantic estuaries and lakes in the northern part of its range. Seasonal movements within the bay are linked to spawning, feeding, and overwintering. The population expanded from the time of its invasion until the early 1970's, when the commercial fishery brought about a slight decline, followed by a climate-related crash in late winter of 1978. Density-dependent growth is clearly demonstrated. Estimates of egg production and survival to age I are made, and biomass and production calculated. A simple simulation model is constructed to test the consistency of the analyses. Early survival estimates are found to be the weak link, primarily because of insufficient data. Available evidence suggests that reduced piscivore abundance, perhaps due to eutrophication, allowed the white perch to proliferate in the bay, where they appear well suited to conditions which are estuarine-like. Recently, it appeared that biomass was declining under the stress of the combined action of a low temperature kill and a resurgence of piscivores, particularly walleye (*Stizostedion vitreum vitreum*). Increased piscivore abundance should prevent white perch recovering to previous levels.

Les auteurs analysent et résument toutes les données disponibles sur l'invasion et la prolifération, pendant les années 1950, du baret (*Morone americana*) dans la baie de Quinte (lac Ontario). Les paramètres vitaux de cette population sont semblables à ceux de l'espèce dans son habitat natal, dans les estuaires de l'Atlantique et dans les lacs septentrionaux de son aire de répartition. À l'intérieur de la baie, les déplacements saisonniers sont liés à la fraie, à la recherche de nourriture et à l'hivernage. La population a augmenté depuis le moment de l'invasion jusqu'au début des années 1970 quand une pêche commerciale a entraîné un léger déclin; la population a été décimée à la fin de l'hiver 1978 suite à des conditions climatiques extrêmes. Une croissance liée à la densité est clairement prouvée. Des calculs de la production d'oeufs, de la survie jusqu'à l'âge I, de la biomasse et de la production sont présentés. Les auteurs ont élaboré un modèle simple de simulation pour vérifier l'uniformité des analyses. Ils ont ainsi découvert que les estimations de la survie au début du cycle vital sont le point faible surtout à cause de l'insuffisance de données. Les preuves disponibles portent à croire que la réduction des piscivores, peut-être causée par l'eutrophisation, a permis au baret de proliférer dans la baie où il semble bien adapté aux conditions presque estuariennes. Récemment, la biomasse a semblé décroître sous l'effet de l'action combinée d'une mortalité entraînée par la basse température et de la réapparition de piscivores, surtout le doré jaune (*Stizostedion vitreum vitreum*). Un plus grand nombre de piscivores devraient empêcher les populations de baret de revenir à leur niveau antérieur.

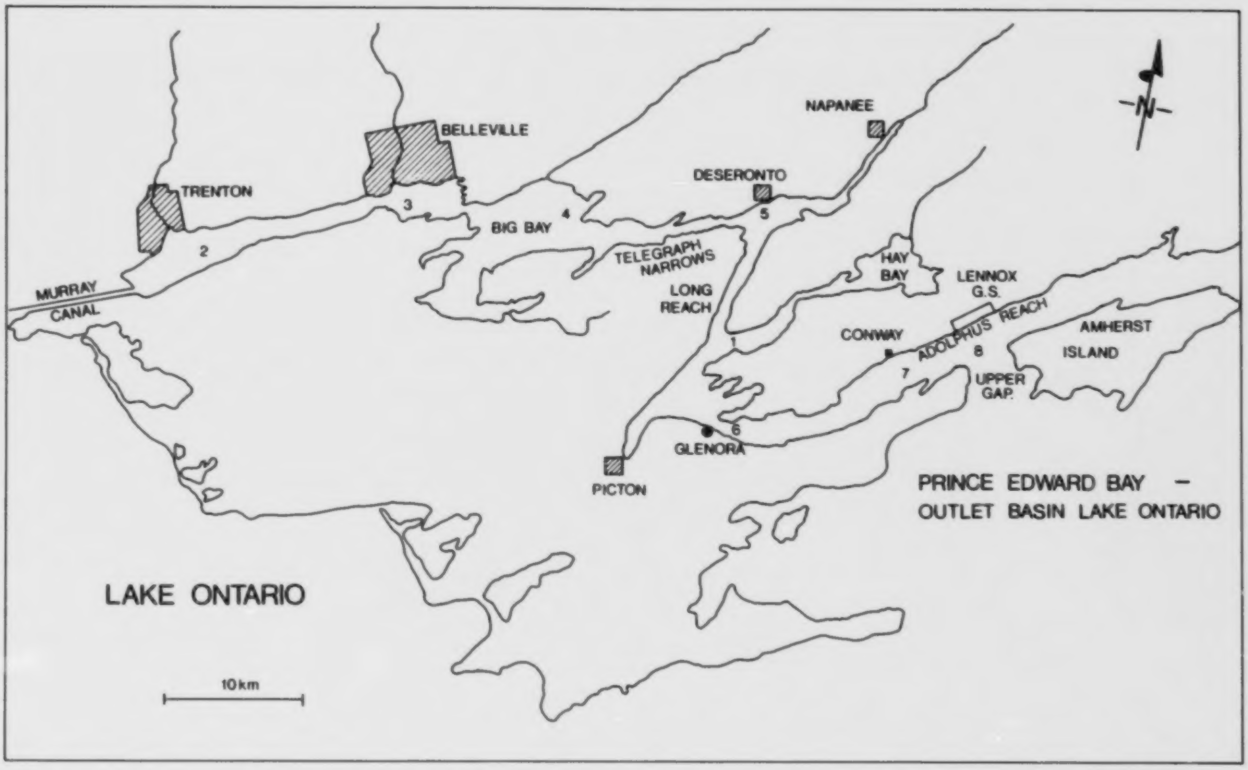
Introduction

The Bay of Quinte is a highly eutrophic embayment of Lake Ontario that grades from a shallow inner zone receiving a substantial nutrient load from sewage treatment plants to a deep outer zone receiving lower nutrient inputs and subjected to incursions of Lake Ontario water during the summer months. The bay is highly productive and yielded a substantial portion of the fish harvest, both commercial and sport, in Lake Ontario.

White perch (*Morone americana*) invaded Lake Ontario via the Hudson River and Erie Barge Canal system about 1950 (Scott and Christie 1963) and proliferated rapidly between then and 1960 (Christie 1973). Since then, they have formed a major portion of the fish biomass up to 1978, when test netting in the summer showed a dramatic reduction in numbers. The extent of the decline can be seen in the commercial harvest, which fell from 200 000 kg in 1978 to 23 000 kg in 1979. No recovery has been noted up to 1981.

In the Bay of Quinte, as white perch numbers increased, their growth rate decreased (Sheri and Power 1972; Hurley 1973). Similar "stunting" has been reported in other freshwater bodies (Thoits 1958; Cooper 1941).

This report examines population trends and distribution, both secular and seasonal, growth rate, size at age, production, and exploitation of white perch from 1958 to 1980. From these data, a simulation model is used to develop a synthesis describing the population dynamics of this species.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MURRAY CANAL
LONG REACH
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CONWAY
ADOLPHUS REACH
AMHERST ISLAND
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UPPER GAP
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GLENORA
PICTON
PRINCE EDWARD BAY – OUTLET BASIN LAKE ONTARIO
LAKE ONTARIO
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FIG. 1. Bay of Quinte showing locations of gillnet sets and trawl tows: 1, Hay Bay gillnet, 1958–80; 2–8, gillnet and trawl sites, 1972–80.

Methods

Species composition and relative abundance has been monitored at Hay Bay, station 1 (Fig. 1), since 1958 using a graded series of gillnet mesh sizes from 3.81 to 11.43 cm in 1.27-cm intervals. Results are reported as the total catch, assuming 91.4 m of each mesh size are fished for one night. Between 1972 and 1980, six additional gillnet fish sites (stations 2–7) were used and catches made monthly from May through August each year.

Between 1972 and 1980, distribution and abundance was also monitored using a three-quarter-sized "Western" polypropylene bottom trawl 19 m long, with 6-m wings and 1.3-cm stretched mesh in the cod-end. This gear was fished over a 0.4-km distance at eight stations (1–8, Fig. 1) in the bay, from Trenton to Lake Ontario. Trawl tows were made monthly from May through to September in each year.

Samples of white perch from these two gear types were taken for length, weight, age, sex, and maturity determinations.

A commercial gillnet fishery operated for white perch in the lower bay below Glenora and was concentrated in the January to March period of each year. Statistics on the catch and effort for various mesh sizes were recorded on a monthly basis for each year.

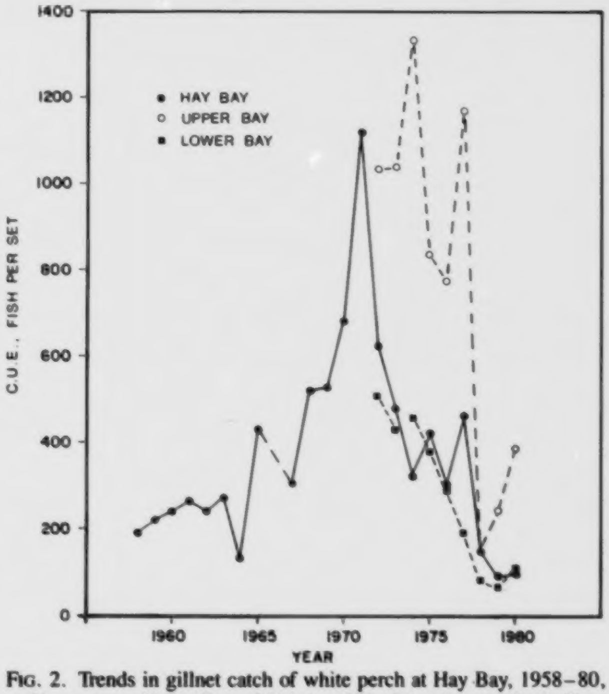

FIG. 2. Trends in gillnet catch of white perch at Hay Bay, 1958–80, and in upper and lower Bay of Quinte, 1972–80, using standard gillnet effort (91.4 m of each of mesh sizes 3.81–11.43 cm in 1.27-cm intervals fished overnight).

Results

Secular Trends

Standard gillnet set-catches at Hay Bay showed an upward trend until 1971, followed by a decline to levels around 400 fish per set between 1973 and 1977 (Fig. 2). In 1978, there was a sharp decline followed by somewhat lower levels in 1979 and 1980. Catches at the seven main stations, 1972–80, follow a similar trend. Catches in the lower bay (stations 6, 7, and 1)

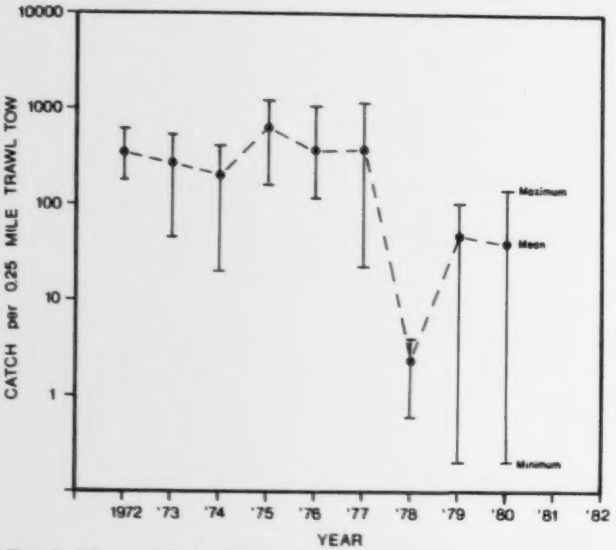

FIG. 3. Mean catch of white perch in standard trawl tows at stations 1–7 in the Bay of Quinte, 1972–80.

were much lower than in the upper bay (stations 2, 3, 4, and 5). All stations showed the sharp decline noted in 1978. Subsequently, both areas of the bay have shown a partial recovery.

Average trawl catches remained relatively constant in the period 1972–77 (Fig. 3). In 1978, a 100-fold decrease was observed, which was greater than the decline observed in gillnet catches. In 1979 and 1980, trawl catches were about 10 times higher than in 1978, but consisted almost entirely of young-of-the-year (YOY).

The commercial gillnet fishery for white perch began in 1960, and increased rapidly. Both effort and catch have been cyclical with peaks in 1965, 1970–71, and 1976–78 (Fig. 4). Catches were usually reported for three mesh size ranges: 5.72–7.62 cm (2¼–3 in.), 7.94–10.80 cm (3⅛–4¼ in.), and 11.43 cm (4¼ in.) and greater. Initially, the mesh composition of commercial nets consisted of 40% of the small size and 60% of the large size (Fig. 4). In 1963, an intermediate size range was introduced to the fishery and gradually replaced the largest mesh size. In the last few years, a small amount of the larger mesh size has reappeared. Since 1971, the quantity of the smallest mesh size has continued to increase until in the early 1980's when it accounted for almost 90% of the total effort. The Bay of Quinte commercial catch of white perch has accounted for most of the total Lake Ontario catch averaging 79% from 1964 to 1975, with a range of 69–90%. This indicates that the Bay of Quinte stock is predominant.

Seasonal Distribution

White perch undertake considerable migrations within the Bay of Quinte. During the winter months (November – April), the population congregated in the lower bay and fish were found throughout the water column. At this time, the commercial fishery was able to catch them when they were most concentrated. This movement to deeper water is similar to that in coastal rivers where white perch move to the estuary in the fall (Thoits 1958).

In spring, adults migrate into the upper bay to spawn. Changes in the number caught per trawl tow and the mean weight of an individual in the catch, by location and month, averaged for 1972–80, illustrate the spring, summer, and fall migrations (Fig. 5). Spawning takes place from the middle of May to the end of June when water temperatures are in the range 11–15°C (Sheri and Power 1968). The mean size of white perch in the upper bay (Trenton – Big Bay) is high in May and June reflecting the presence of adults, while mean size elsewhere is lower, suggesting that immature fish remain in the lower bay during the spawning period (Fig. 5).

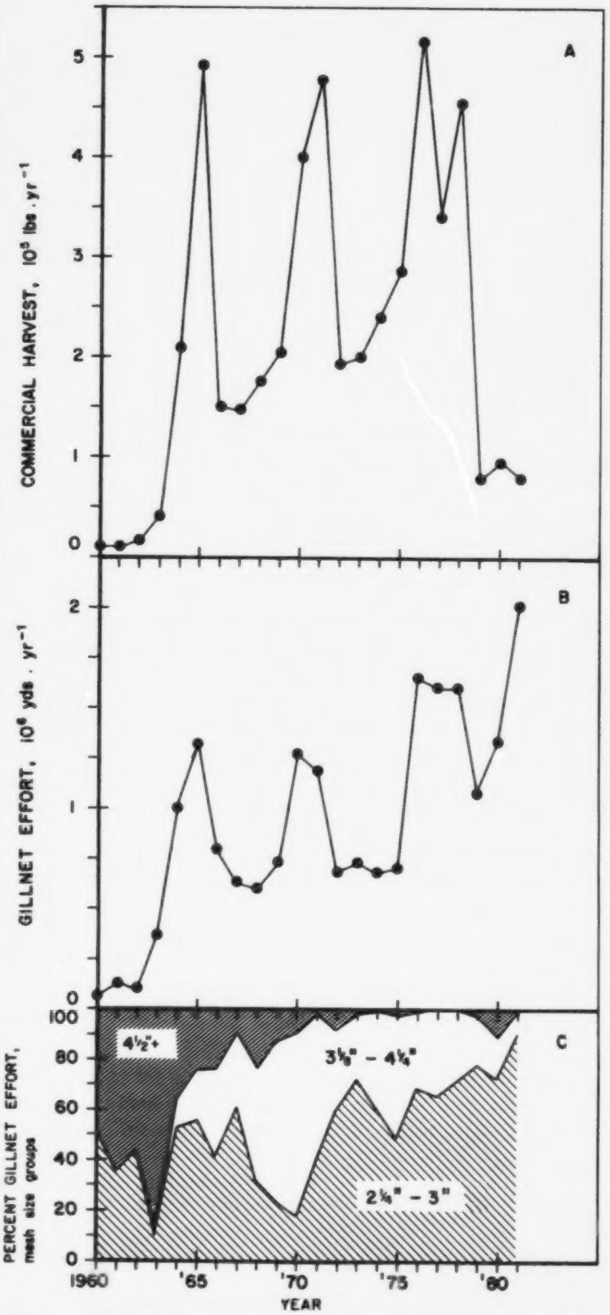

FIG. 4. Trends in (A) commercial harvest, (B) gillnet effort, and (C) allocation of effort by gillnet mesh size for white perch in the Bay of Quinte.

YOY first appear in trawl catches in late July to early August; the total number per tow increases in the upper and middle bay areas and the mean size may start to decline (Fig. 5). YOY

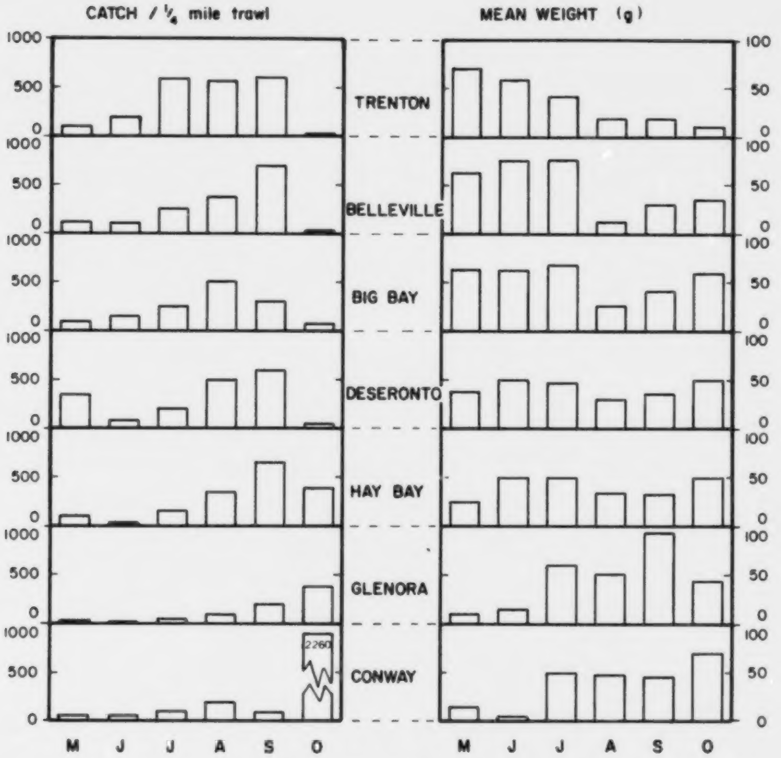

FIG. 5. Mean monthly trawl catch and average weight of individuals from sites in the Bay of Quinte from the upper bay (Trenton) to the lower bay (Conway), 1972–80.

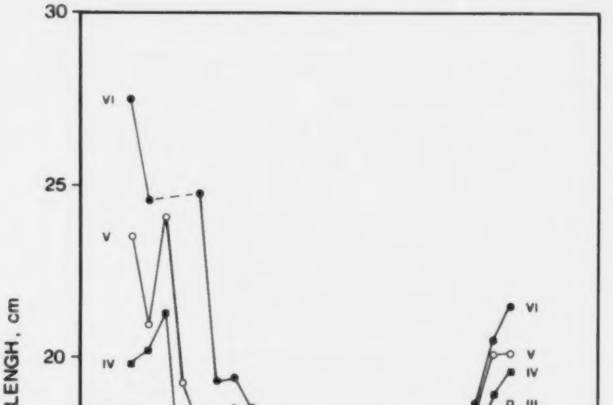

FIG. 6. Length at age for white perch over the period 1958–80.

dominate in August (37.9%) and September (24.2%) catches from Hay Bay on up the bay; the number per tow increases and the increase in numbers of YOY decreases the mean weight per individual in the catch.

Meanwhile, after spawning, it appears that adults disperse throughout the bay, since mean size increases at Glenora and Conway in July. In October, catches decline in the upper bay, while they increase to their highest levels in the lower bay, reflecting the fall migration of white perch to deeper waters. Mean size at this time returns to average spring levels which could result from both YOY growth and the high mortality of YOY fish relative to older fish.

Growth

The size, and therefore growth, of age II and older white perch varied inversely with abundance between 1958 and 1980 (Fig. 6). In recent years, the observed lengths of age II–IV fish have shown the expected response to lower stock abundance, while older fish have not responded. This difference is likely due to the continued selective removal of more rapidly growing individuals vulnerable to the intensive gillnet fishery in the recent period.

We fitted a multiple regression model of growth for fish aged II–VI, but not for older fish, as annual growth increments from age VI–VIII were inconsistent. The inconsistency was likely due to low sample sizes. We obtained the following equation:

$$(1) \quad \log_e L_{ij} = 0.85 + 0.736 \log_e L_{i-1,\, j-1} - 0.00009 N_j$$

where L_{ij} is the mean length (centimetres) of fish age i in year j and N_j is the mean catch (number) per standard gillnet at Hay

Bay in year j (Fig. 2).

The overall regression was significant ($P = 0.01$) ($F = 215.6$ on 2,88 df, multiple $r = 0.91$). The coefficients of both independent variables were significantly different from zero, $t_1 = 19.43$ ($\log_e L$) and $t_2 = 3.16$ (N). Neither growth increments nor the residuals of the above regression were found to be correlated with either the mean summer temperature or the mean May temperature, which was the most variable month, as recorded at the water intake of the Belleville filtration plant in the upper bay (Fig. 1).

As noted above, fishing probably modifies the size composition of the population by selectively removing the larger sized individuals. This would tend to minimize the observed effect of density on growth. At low stock abundance, faster growing fish will recruit younger to the fishery and thus would not be available for observation at more advanced ages. Fish appear to be fully recruited to the fishery at 18–19 cm (see Table 4) which would have left only age groups III and IV unaffected by fishing in the period 1967–77.

It appears that YOY growth from the end of July through to October is dependent on temperature and density of YOY. The hatchery growth model for young fish described by Iwama and Tautz (1981) provided a good description of temperature-dependent growth:

$$(2) \qquad W_t = (W_0^k + t \cdot f(T))^{1/k}$$

where W_0 and W_t are weights (grams) at time 0 and t days, respectively, and $f(T)$ is a function of temperature T (Celsius) and k is a constant.

The model was fitted in the form

$$(3) \qquad Y = (W_t^k - W_0^k) / t = a + bT$$

where a and b are regression coefficients. We assumed that W_0 was 0.00115 g, the average weight of a white perch egg (Sheri and Power 1968). By iteration, the best value of k was found to be 0.755 and the regression result was

$$(4) \qquad Y = -0.0528 + 0.00439T.$$

The correlation was significant ($r = 0.88$, $N = 12$) returning it to the form of equation 2:

$$(5) \qquad W_t = [W_0^{0.755} + t(-0.0528 + 0.00439T)]^{1/0.755}.$$

The residuals from equation 4 were correlated with the August YOY catch per trawl tow (N_{yoy}). We fitted a multiple regression equation:

$$(6) \qquad Y = -0.0243 + 0.00457T - 0.0065 \log_e N_{yoy}.$$

The overall regression was significant ($P = 0.01$), $F = 28.9$ on 2,9 df, multiple $r = 0.93$. The coefficients of both independent variables were significantly different from zero, $t_1 = 7.32$ (T) ($P = 0.01$) and $t_2 = 2.48$ ($\log_e N_{yoy}$) ($P = 0.05$). This result is a typical link found for YOY growth in fishes (Backiel and LeCren 1978); higher than average temperatures produce better growth, while greater numbers result in greater competition for food and reduced growth.

Population Dynamics

The trawl catch for August was used for more detailed analysis, because catches were generally highest in this month and fish of all sizes including YOY seemed to be more evenly distributed throughout the bay in this month. For each of the years 1972–80, the average bay-wide August catch per trawl tow was calculated.

The age composition was determined from the length frequencies in the catch combined with an age–length key developed using samples from August gillnet and trawl catches. Trawl catches were used instead of gillnet catches to determine population statistics because a wider size range of fish was present.

Examination of the age frequency data obtained from the trawl catches suggested that, on average, white perch were not fully vulnerable to the trawl until age V (Table 1). Since the data were limited, the data for 1972–80 were combined and average annual survival rates were calculated for age V and older fish. The survival rate for age V of 0.44 was consistent with average survival rates in unexploited age classes of other populations, i.e. 0.45 in Patuxent Estuary and 0.44 in the Delaware River, reported by Mansueti (1961) and Wallace (1971), respectively. During the period 1972–80, white perch started to be harvested by the commercial fishery at age VI (compare Fig. 6 and Table 3), and the survival rates for age VI and older fish are consistent with that level of exploitation. Recent spring commercial catch data support the idea of knife-edge recruitment to the fishery. In 1978, 6.5% of the catch was age IV or less compared with 26.5% at age V; in 1979, 5.8% of the catch was age III compared with 59.7% age IV; and in 1980, 2.2% was age III compared with 48.6% age IV.

For further analysis, we assumed that the survival rate for age V fish also applied to younger year classes. Mean population numbers were extrapolated back for each age, and a multiplier (X) was calculated from the ratio of extrapolated count to observed mean (Table 1). These results were then used to estimate the survival from egg stage to age I for each year class using the following analysis:

$$(7) \qquad N_{Ij} = N_{yoy} \cdot X_0 \cdot S$$

where N_{Ij} is the number of survivors to age I of the year class born in year j, N_{yoy} is the number of YOY in August trawls of year j, S is average natural survival rate (0.44), and X_{yoy} is the multiplier.

Egg production was estimated by the equation

$$(8) \qquad E_j = 0.5 \sum_{j=2}^{9} N_{ij} \cdot X_i \cdot aW_{ij}^b$$

where 0.5 is the sex ratio, aW^b is the fecundity equation calculated from data of Sheri (1968), $a = 34.5$, $b = 1.492$, N_{ij} is number of fish of age i in year j in the average August bay-wide trawl catch (Table 1), W_{ij} is weight (grams) of fish age i in year j, and X_i is the multiplier for age i.

Thus

$$(9) \qquad \text{Survival from egg to age } I = N_{Ij} / E_j.$$

Survival rates from egg to YOY August and from YOY August to age I cannot be separated. The trawl catch curve is strongly affected by selectivity at the low size end, only the cod-end being able to retain YOY and age I fish. However, the YOY and age I means trawl catches 140.2 vs. 21.9 (Table 1), gives a nominal survival estimate of 0.21, which suggests that most YOY mortality has occurred by August.

The egg to age I survival rates (S_{01}) range from 0.0000275 to 0.00124 with a geometric mean of 0.000236 (Table 1). The rates were correlated with egg numbers (E_j) and mean May water temperatures at Belleville (T_j), singly and together:

$$(10) \qquad \log_e S_{01j} = -6.86 - 0.062E_j\,(10^{-6})$$

$$(11) \qquad \log_e S_{01j} = -21.68 + 0.911T_j\,(C)$$

$$(12) \qquad \log_e S_{01j} = -19.00 - 0.0995E_j + 0.768T_j.$$

TABLE 1. Population structure of white perch in August trawl catches in the Bay of Quinte.

Year	Total[a]	Age 0	I	II	III	IV	V	VI	VII	VIII	IX	Estimated egg production (10^6)	Survival egg to age I	May temperature (°C)
1972	499.0	65.7	15.4	64.9	152.9	132.1	43.1	15.8	6.3	1.7	1.1	14.20	0.0000449	13.0
1973	327.3	35.6	7.1	9.7	63.4	116.9	72.1	21.2	1.4	0	0	6.00	0.0000571	13.0
1974	356.3	0	12.5	43.9	87.8	84.1	86.1	31.6	8.3	1.8	0.2	10.51	—	12.9
1975	1052.6	687.1	4.0	28.3	31.4	77.0	137.3	72.7	14.3	0.5	0	7.39	0.0009030	16.6
1976	465.0	21.3	150.3	16.2	63.5	64.8	91.7	46.2	10.4	0.4	0.4	7.51	0.0000275	12.6
1977	344.6	224.3	0.4	19.9	8.8	29.7	33.8	20.7	5.0	0.7	0	3.99	0.0005420	16.3
1978	2.5	0	0.6	0	1.9	0	0	0	0	0	0	0.08	—	13.9
1979	155.4	132.2	5.6	1.8	0.1	13.8	0.5	0.6	0.4	0.2	0.1	1.02	0.0012400	15.6
1980	110.1	97.0	1.4	2.4	1.5	0.4	6.7	0.1	0.2	0.1	0	1.01	0.0009210	15.3
Mean *A*		140.2	21.9	20.8	45.7	57.6	52.4	23.2	5.1	0.6	0.2			
Annual survival(s)		—	—	—	—	—	0.4432	0.2216	0.1166	0.3333				
Extrapolated population *B*		3064.3	1358.1	601.9	266.8	118.2	52.4	23.2	5.1	0.6	0.2			
Multipliers *B*/*A*		21.83	62.01	28.94	5.84	2.05	1	1	1	1	1			

[a] Numbers per August trawl tow.

TABLE 2. Predicted size (g) of YOY after 150 d for combinations of egg production per August trawl tow and average May temperature. Given: mean summer temperature TS = 15 + TM/3; $N_{yoy} = E \cdot S_{01}/S/X_{yoy} = E_1$ equation 12/0.44/21.83 (Table 1); $W_{153} = (W_0^{0.755}$ + equation $6^{1/0.755}$; growing season assumed to be 153, midrange of 134–173 d above 13°C, the midpoint of the spawning range.

Egg production, *E* (10^{-6})	May temperature, TM (°C) 11	13	15	17
1	16.9	11.2	11.5	9.0
5	13.8	10.7	8.7	6.4
9	13.3	10.8	8.3	6.0
13	13.7	11.1	8.3	6.1
17	14.1	11.5	8.6	6.3

The regression with E_j (equation 10) was barely significant ($F = 4.8$ on 1,5 df, $r = 0.70$). The regression with T_j (equation 11) was highly significant ($F = 36.4$ on 1,5 df, $r = 0.94$). Temperature is a better predictor of survival than egg numbers. Furthermore, in 1974 when YOY were not detected, indicating low egg survival, the May temperature was low. Survival in 1978 was undetermined because low egg production gave rise to an undetectable level of YOY. The multiple regression (equation 12) was marginal improvement over equation 11 ($F = 27.7$ on 2,4 df, multiple $r = 0.97$). Only one slope, for T_j, was significantly different from zero ($t - b1 = 1.8$, $t - b2 = 5.1$).

The S_{01} survival rates and YOY growth combine to bring about a similar size by the fall from year to year over much of the combined ranges of egg production (5×10^6 to 9×10^6) and May temperature (13–15°C) (Table 2). The combination of equations indicates that the best growth is achieved with low temperature and low egg densities. At higher egg densities and higher temperatures, growth declines as the absolute number of survivors increases. At the highest egg densities the number of survivors decreases and growth increases again.

Production

The production of white perch was calculated given the following assumptions.

(1) A trawl sweeps 0.2453 ha per 0.4-km tow.

TABLE 3. Calculation of production of white perch in the Bay of Quinte

Age	Density (ha^{-1})[a]	Weight (g)[b]	*G*	*Z*	Biomass (kg · ha^{-1})	Production (kg · ha^{-1})
0	42.7×10^6	0.00115	9.84	9.52[c]	49.0	569.8
I	5536.5	21.6	0.70	0.81	119.6	78.3
II	2453.7	43.3	0.39	0.81	106.2	33.9
III	1087.6	64.0	0.27	0.81	69.6	14.55
IV	481.9	83.9	0.14	0.81	40.4	4.20
V	213.6	96.7	0.20	0.81	20.7	3.14
VI	94.6	118.5	0.17	1.51	11.2	1.02
VII	20.8	139.7	0.33	2.15	2.9	0.45
VIII	2.4	193.9	0.36	1.10	0.5	0.12
IX	0.8	276.6	0.36	1.10	0.2	0.04
Total					420.3	705.5

[a] Trawl sweeps 0.2453 ha per 0.4-km tow.

[b] Ages II–IV average weight used; age I assumed to be one-half of age II; egg weight from Sheri and Power (1968).

[c] Estimated from regression of survival on density.

(2) The number of individuals, i.e. eggs, could be calculated from the egg production of age II and older fish, and the regression of survival to age I on egg density could be used to estimate *Z*, the mortality coefficient.

(3) For ages II – IX, average weights in 1972–80 could be used, and weight at age I was half that at age II. The weight at age I averaged 0.6 of that at age II (SD = 0.186, $n = 15$) for August gillnet catches, 1958–80. This was most likely an overestimate given the size selectivity of gillnets, so 0.5 was used instead.

(4) *Z* for ages I – V was 0.81 ($-\log_e S$ where $S = 0.44$), representing natural mortality only.

(5) *Z* for ages VI – IX could be taken from the survival values in Table 1 and assumed to be the sum of natural mortality ($M = 0.81$) and fishing mortality (*F*).

(6) Production was estimated for each age class by the formula

$$P = G\bar{B}; \bar{B} = B_0 \frac{(e^{G-Z} - 1)}{G-Z} \text{ (Ricker 1975).}$$

(7) Weight of an individual egg at age 0 was 0.00115 g, calculated from data of Sheri and Power (1968).

Table 4. Relative catchability of white perch in commercial gillnets (based on sample data collected by Lake Ontario Fishery Assessment Unit, OMNR).

Size range (cm)	2½–3 in.	3⅛–4¼ in.	4½ + in.
15–15.9	0.01	0.01	0
16–16.9	0.17	0.02	0
17–17.9	0.63	0.09	0
18–18.9	1.00	0.44	0.01
19–19.9	0.97	1.00	0.02
20–20.9	0.57	0.95	0.13
21–21.9	0.30	0.57	0.54
22–22.9	0.11	0.31	1.00
23–23.9	0.05	0.15	0.96
24–24.9	0.02	0.10	0.30
25–25.9	0.01	0.07	0.13
26–26.9	0.00	0.06	0.10
27–27.9	0.00	0.06	0.06
28–28.9	0.0	0.06	0.06
29–29.9	0.0	0.04	0.04

The mean initial population biomass (B_0), 1972–80, was estimated to be 420 kg · ha^{-1} and production was 705.5 kg · ha^{-1} · yr^{-1} (Table 3). The production to biomass ratio of 1.68 is similar to those quoted by Chapman (1978) for a wide variety of fish species. The average yield portion of production was calculated using the estimated fishing mortality rates ($F = Z - M$) for ages VI – IX, and multiplied by 25740, the bay area in hectares. The predicted yield of 160 000 kg · yr^{-1} is slightly higher than the commercial yield for 1972–80 which averaged 121 500 kg · yr^{-1}.

Simulation Model

A simple population model was constructed, using the results and relationships developed above, to examine their consistency and predictiveness.

Natural and Fishing Mortality

We assumed the natural mortality coefficient (M) was 0.814 for age I and older fish. This mortality was assumed to occur during the winter, concurrent with fishing mortality (F). Partitioning M over all seasons would not make much difference. Fishing mortality (F) was a function of effort (f), absolute catchability (q), and relative size catchability (r):

$$F = f \cdot q \cdot r \cdot$$

Relative catchability by size was estimated, for the three mesh size ranges in the commercial fishery, from length frequency data obtained from samples of the commercial catch (Table 4). Absolute catchability was calculated using the commercial gillnet catch-per-unit-effort (CPUE) and the Hay Bay experimental gillnet catch series, 1960–80.

The average ratio of Hay Bay gillnet catches to August trawl catches (4.2903) was used to scale the gillnet catches to trawl equivalents, which were then converted to per unit of bottom area (hectares). The age frequency and size at age data for these gillnet catches were combined with the relative catchabilities to calculate the vulnerable population size for each of the three commercial mesh size ranges. Harvest of white perch was converted from weight to number using an individual fish weight corresponding to the peak relative catchability. Absolute catchability (q) was calculated as follows:

$$q = \log_e (1 - \text{harvest} / \text{population}) / \text{effort}.$$

Table 5. Absolute catchability (q) estimates.

Mesh size range (cm)	N	$\log_e$ mean	SD	Exp (mean) = q
5.72–7.62	20	− 12.587	± 4.455	$3.416 \cdot 10^{-6}$
7.94–10.80	17	− 12.215	± 3.109	$4.955 \cdot 10^{-6}$
11.43 +	17	− 13.531	± 8.032	$1.329 \cdot 10^{-6}$

The values obtained for the period 1961–81 are highly variable (Table 5). The values for the small and medium mesh ranges are negatively correlated with population abundance, $r = -0.289$ and $r = -0.400$, respectively.

Reproduction

Sheri (1968) presented data that indicated that females were first mature at a weight of 37.4 g and that all fish were mature at a weight of 97.5 g. We assumed a 50:50 sex ratio. Spawning occurred in May and June. The fecundity curve (aW^b calculated from data of Sheri 1968) used in the survival and production calculations was employed.

Growth

Growth was predicted using the regression obtained above (equation 1). The density parameter in equation 1 was adjusted to represent the effect of density on a unit area basis (N = number per area, age I and older):

$$\log_e L_{t+1} = 0.736 \log_e L_t + 0.85 - 5.15 \cdot 10^{-6} \cdot N. \qquad (13)$$

Survival and Growth of YOYs

These variables were predicted using the regression equations 5, 6, 10–12 presented above. Growth was assumed to begin at 13°C, the midpoint of the spawning temperature range, 11–15°C, quoted by Sheri and Power (1968). Duration of the growth season was the number of days that the temperature exceeded 13°C. The water temperatures used were those taken daily at the Belleville filtration plant. The growth temperature was calculated as the mean of temperatures during the growth season. The growth season ranged from 134 to 173 d and the growth temperature ranged from 18.9 to 21.5°C during the period 1950–80.

Initial Conditions

To begin simulations, a small population of white perch was assumed to appear in the bay in 1950. Necessary temperature data — mean May temperature, growing season, and growth temperature — were calculated for 1950–80. The recorded fishing effort was applied from 1960 on. A 95% mortality was applied at 1978 to mimic the observed winterkill.

Simulation Results

The first simulations using all the parameter estimates produced unrealistic results. In all cases, the difficulty lay in the prediction of survival from egg to age I. If the multiple regression involving egg density and spring temperature was used, the model predicted recruitment that was highly variable. If the regression involving egg density alone (equation 10) was used, the model failed to produce sufficient recruits.

The parameters of the egg survival equation involving egg density were altered iteratively until the model behaviour appeared reasonable. Using the following equation:

$$\ln \text{survival} = -5.00 - 0.2 \text{ eggs} \cdot 10^{-6} / \text{ha} \qquad (14)$$

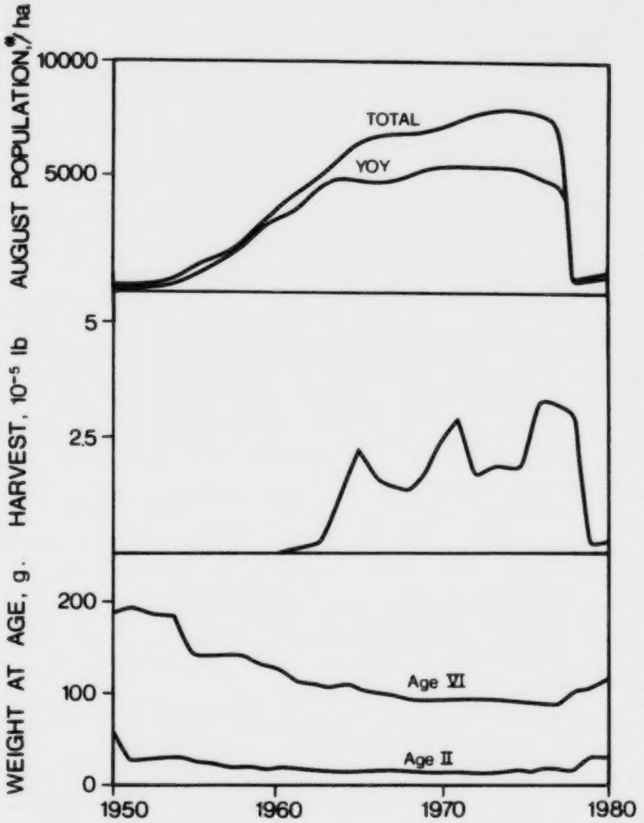

FIG. 7. Simulation results over 30 yr based on assumptions that produce the closest fit to observed results of population size, harvest, and fish size at age.

a set of predictions was obtained (Fig. 7) which agree reasonably well with the data. Thus it was necessary to increase the maximum survival from 1:953 to 1:148 and to make the density-related decline in survival much more strongly dependent on egg density.

The uncertainty associated with estimates of early survival is a general problem in fisheries ecology. In this case, it stems from the survival data set being limited. However, if estimates for all the other parameters in such a simple model are judged acceptable, one can use a model and expected results to arrive at reasonable estimates of early survival.

The model describes the population growth and exploitation up to the late 1970's adequately. Recent observations suggest that the model may need modification to predict future response. White perch have not recovered from the crash they suffered in 1978 and the model predicts that if current high levels of fishing effort persist, white perch will recover only slowly.

In addition, walleye (*Stizostedion vitreum vitreum*) prey upon white perch in the Bay of Quinte (Hurley and Christie 1977; Hurley 1986a), although not to the degree that they eat alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*). In 1978, an exceptionally strong year class of walleye developed in the bay. It is believed that these fish, because of sheer numbers, significantly impacted the white perch in the bay. Forney (1977) has suggested that moderate predation by a large walleye population controls white perch in Oneida Lake, though alewives are absent in that situation. The likely prognosis for the white perch in the Bay of Quinte is that continued heavy fishing combined with a low level of predation by a large walleye stock will keep white perch well below previous levels of abundance.

Discussion

The rise of white perch in the Bay of Quinte occurred rapidly from the time of their first appearance in 1952 to their position of dominance in the early 1960's (Scott and Christie 1963). Their numbers continued to rise until the early 1970's. A decline in abundance was noticeable after 1972 and a pronounced "crash" occurred in the spring of 1978. Since then the population has not recovered.

The effect of the commercial fishery is hard to define, but removal of an average 120 000 $\mathrm{kg \cdot yr^{-1}}$ appears to have been sufficient to prevent further population increase after the early 1970's. The decline in the growth rate during the period of population expansion points strongly to some form of competition in that period. However, the harvest of white perch was apparently never sufficient to depress the population enough to cause an increase in growth rates. As the fishery developed, the older age classes were reduced by removal and the younger age classes (II – V) increased, maintaining the density effect on growth. Growth rates increased sharply after the 1978 crash when the population was decimated.

The dramatic decline that occurred in 1978 has been linked to below-average late winter water temperatures in the lower bay (Hurley 1986a). Many dead white perch were observed in trawl catches in the lower bay area in the spring of 1978 (R. C. McIntosh, Glenora Fisheries Station, pers. comm.). Such a mortality is consistent with the fact that white perch in this area are near the northern limit of their distribution. Thus, they may be exposed to a "fringe" effect (Wynne-Edwards 1962), which states that physical conditions can control populations at the limits of their distribution.

Although white perch are present throughout Lake Ontario, they rose to dominate the fish community only in the Bay of Quinte. This may be due to the morphological features of the bay which provide extensive shallow areas, lentic conditions, and warm temperatures (22–25°C) for most of the summer in the upper bay for spawning and feeding, and deep waters in the lower bay where white perch congregate in winter, as they do in the estuaries along their home range on the Atlantic coast (Thoits 1958).

The bay was subjected to increasing nutrient loading over the period of white perch expansion (Minns 1986). Hurley and Christie (1977) suggested that eutrophication stressed the piscivore community which in turn permitted white perch to avoid control by predators. There is no evidence, however, to suggest that eutrophic conditions directly enhanced the white perch invasion and subsequent increase.

In the late 1950's and 1960's the main piscivores, particularly walleye, were decreasing in abundance, while white perch were increasing. Conversely, in West Lake (Hurley and Christie 1977) and Oneida Lake (Forney 1977), where white perch invaded at about the same time, the species was able to establish itself, but unable to dominate in the presence of large piscivores. In Oneida Lake, Forney was able to explain this by way of heavy walleye predation on white perch, except for years when yellow perch year classes were strong. This took place in the absence of alewife. In the bay, alewife were present and were (and are) a principal prey of walleye; thus, walleye predation of white perch is relatively slight. The simulation model indicated that moderate predation (or exploitation) would be sufficient to hold numbers of white perch down when their population is low.

Although the predation "picture" appears simple, competition effects appear to be more complex. There is clear evidence of "stunting" in the bay's population of white perch, and similar occurrences have been noted in other white perch invasions of freshwater systems (Sheri and Power 1972). While white perch and yellow perch (*Perca flavescens*) in the bay share roughly the same diet (Hurley 1986b), there is no evidence of matching declines in the growth of yellow perch. In the upper bay, their diets are made up almost entirely of chironomids, whereas in the lower bay there are significant proportions of crustaceans: isopods, gammarids, and *Pontoporeia*. Stunting is most simply explained as food limitation and it appears that white perch are food-limited, while yellow perch are not.

A likely explanation for the differences in growth response of these two species may be the fact that while they share the same feeding locations, they feed at different times of day. White perch appear to feed more at midday and midnight (Leach 1962), while yellow perch feed at dawn and dusk (Keast and Welsh 1968). Yellow perch are rarely caught in daytime offshore trawling where white perch are abundant, while both species are common in nearshore overnight gillnet catches. Yellow perch must venture offshore at some time, since it is from there that they obtain the bulk of their food (Hurley 1986b).

White perch appear to be well suited to conditions prevailing in the Bay of Quinte. A depression of the main piscivores appears to have allowed the proliferation of the species, to the point where a large commercial exploitation was possible. However, recent events have gone against white perch. A dramatic late-winter mortality decimated the population, and concurrently there has been an upsurge in piscivores, particularly walleye. Current evidence points to the persistence of white perch in the Bay of Quinte, although at more modest levels than in the past.

Acknowledgements

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References

Backiel, T., and E. D. LeCren. 1978. Some density relationships for fish population parameters, p. 279–302. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

Chapman, D. W. 1978. Production in fish population, p. 5–25. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

Christie, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. No. 23: 65 p.

Cooper, G. P. 1941. A biological survey of lakes and ponds of the Androscoggin and Kennebec River drainage systems in Maine. Fish Surv. Rep. 4: 1–238. Maine Department of Inland Fish and Game.

Forney, J. L. 1977. Evidence of inter- and intra-specific competition as factors regulating walleye (*Strizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34: 1812–1820.

Hurley, D. A. 1973. Some post-invasion changes in the white perch, *Morone americana* (Gmelin), of the Bay of Quinte, Lake Ontario. File Report No. 2-73. 20 p. Glenora Fisheries Station, Picton, Ont.

1986a. Fish populations in the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. Effect of nutrient reduction on the diets of four fish species in the Bay of Quinte, Lake Ontario, p. 237–246. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Hurley, D. A. and W. J. Christie. 1977. Depreciation of the warm-water fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Iwama, G. K. and A. F. Tautz. 1981. A simple growth model for salmonids in hatcheries. Can. J. Fish. Aquat. Sci. 38: 649–656.

Keast, A., and L. Welsh. 1968. Daily feeding periodicities, food uptake rates and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. 25: 1133–1144.

Leach, J. F. 1962. Summer food and feeding of the white perch *Roccus americanus* (Gmelin) in the Bay of Quinte. M.A. thesis, University of Toronto, Toronto, Ont.

Mansueti, R. J. 1961. Movements, reproduction and mortality of the white perch, *Roccus americanus* in the Patuxent Estuary, Maryland. Chesapeake Sci. 2: 142–205.

Minns, C. K. 1986. Total phosphorus loading to the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Scott, W. B., and W. J. Christie. 1963. The invasion of the lower Great Lakes by the white perch, *Roccus americanus* (Gmelin). J. Fish. Res. Board Can. 20: 1189–1195.

Sheri, A. N. 1968. Growth dynamics of white perch, *Roccus americanus*, during colonization of Bay of Quinte, Lake Ontario. Ph.D. thesis, University of Waterloo, Waterloo, Ont. 366 p.

Sheri, A. N., and G. Power. 1968. Reproduction of white perch, *Roccus americanus*, in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 25: 2225–2231.

1972. Effect of density on the growth of white perch, *Roccus americanus* (Gmelin), in the Bay of Quinte, Lake Ontario. Pak. J. Zool. 4: 109–132.

Thoits, C. F. 1958. A compendium of the life history and ecology of the white perch *Morone americana* (Gmelin). Fisheries Section, Mass. Div. Fish. Game, Fish. Bull. No. 24.

Wallace, D. C. 1971. Age, growth, year class strength and survival rates of the white perch, *Morone americana* (Gmelin) in the Delaware River in the vicinity of Artificial Island. Chesapeake Sci. 12: 205–218.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh and London.

Growth, Diet, and Food Consumption of Walleye (*Stizostedion vitreum vitreum*): An Application of Bioenergetics Modelling to the Bay of Quinte, Lake Ontario, Population[1]

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Hurley, D. A. 1986. Growth, diet, and food consumption of walleye (*Stizostedion vitreum vitreum*): an application of bioenergetics modelling to the Bay of Quinte, Lake Ontario, population, p. 224–236. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Energy requirements for the large 1978 year-class of walleye (*Stizostedion vitreum vitreum*) are calculated from their observed growth in each year from 1978 through 1983. Two models of energy expenditure are examined. One estimates the energy for growth and projected energy for reproductive products from age 3 through age 10. The other uses published bioenergetics values for prey caloric density and predator caloric density, plus observed values for prey weight, diet composition, and temperature to estimate prey consumption that results in the observed walleye growth. Estimates of prey production are calculated and appear adequate for all species except alewife (*Alosa pseudoharengus*). Migration of large numbers of prespawning alewife each spring into the bay from Lake Ontario replenishes the population. Daily energy intake from the model is generally in the range reported from other studies but is considerably less than that calculated from field data from the bay.

Les besoins énergétiques de l'importante classe d'âge de doré jaune (*Stizostedion vitreum vitreum*) de 1978 sont calculés à partir des taux de croissance observés chaque année de 1978 à 1983. L'auteur étudie deux modèles de dépenses énergétiques. L'un permet d'estimer l'énergie nécessaire à la croissance et de prévoir celle nécessaire aux produits de la reproduction pour les âges 3 à 10. L'autre fait appel aux valeurs bioénergétiques publiées relatives à la densité calorique des proies et des prédateurs ainsi qu'aux valeurs observées du poids des proies, de la composition du régime alimentaire et de la température, pour estimer la consommation des proies qui se traduit par la croissance observée chez les dorés. L'auteur a calculé des estimations de production de proies qui semblent adéquates pour toutes les espèces, sauf le gaspareau (*Alosa pseudoharengus*). Chaque printemps, la migration vers la baie d'un nombre élevé de gaspareaux pré-géniteurs en provenance du lac Ontario reconstitue les effectifs de la population. L'absorption quotidienne d'énergie indiquée par le modèle se situe généralement dans la gamme signalée dans d'autres études, mais elle est considérablement inférieure à celle calculée à partir des données recueillies dans la baie.

Introduction

Walleye (*Stizostedion vitreum vitreum*) was a major commercial and sport fishery species during the 1950s and early 1960s in the Bay of Quinte, but their numbers declined drastically after the mid-1960s. The demise of walleye was attributed to the effects of the rise of an invading species, white perch (*Morone americana*), and the steadily decreasing water quality of the bay which was the result of nutrient enrichment (Hurley and Christie 1977).

Walleye abundance, however, began increasing in 1977 and especially in 1978, when an unusually strong year-class developed. Young-of-the-year (YOY) walleye were captured in standard trawling gear in large numbers, and fishermen reported large catches in the late summer and fall of 1978. The resurgence of walleye was attributed to the combined effects of improvement in water quality and the drastic reduction in white perch in the spring of 1978 (Hurley 1986).

The reestablishment of walleye, not only as a major species of commercial interest, but also as a major piscivore, heralded a dramatic change in the bay from a fish assemblage of small-sized benthivores and numerous planktivores, to one where large-sized predators formed a significant component of the bay ecosystem.

The purpose of this paper is to describe the diet of walleye from YOY to adult and, through a bioenergetics model, to simulate the consumption of prey items of the 1978 year-class from age 0 through age 5. Because maximum gonad size and maturation of all females of the 1978 year-class was only partially developed by 1983, a subsidiary purpose was to estimate the projected growth in somatic and gonadal tissue during the lifetime of this year-class using a model proposed by Ware (1980).

Finally, the estimated production of walleye prey was developed from trawling and trapnet data for fish species and from plankton and dredge hauls for invertebrates. The estimated consumption and production of prey were compared in the manner proposed by Stewart et al. (1981, 1983).

Methods

Collections and Fish Examination

Walleye were obtained from standard gillnet sets at up to nine locations in the Bay of Quinte from Trenton in the upper bay to Conway in the lower bay (Fig. 1). Nets were set at monthly intervals from May through August in the late afternoon and

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[1] Contribution 85-05, Ontario Ministry of Natural Resources, Fisheries Branch, Maple, Ont. L0J 1E0.

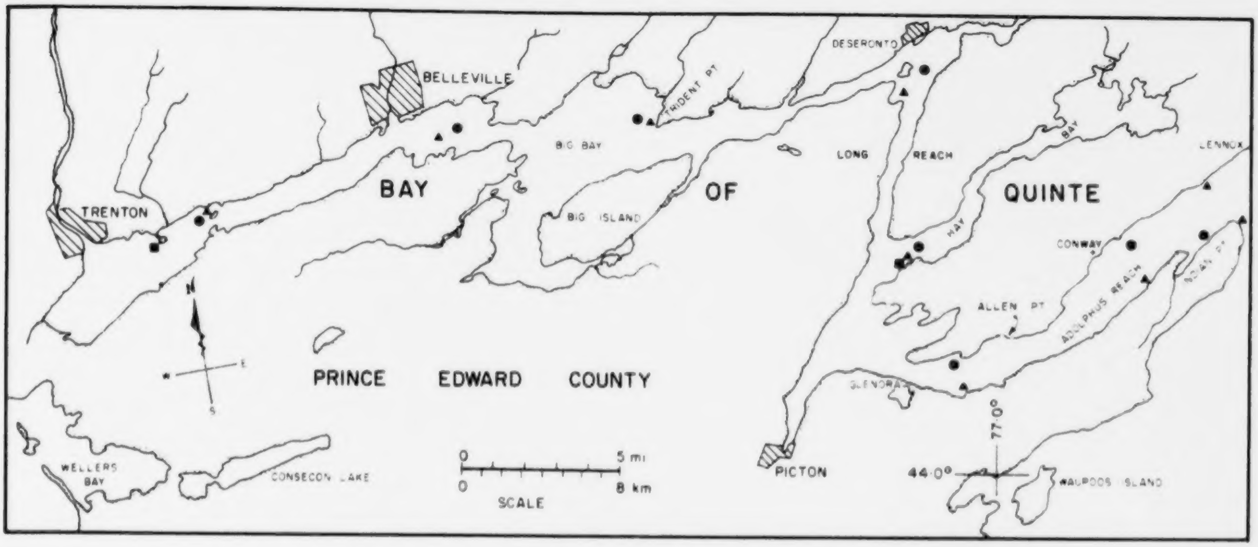

FIG. 1. Bay of Quinte showing sites of trawl drags (●), gillnet sets (▲), and trap nets (■).

lifted the following morning (16–20 h set duration). Some nets were set for shorter durations (3–12 h). A standard gillnet consisted of panels of mesh sizes from 3.8 cm through 11.4 cm in increments of 1.3 cm. The lengths of panels ranged from 22.9 m for smaller mesh sizes to 45.7 m for larger sizes, joined to form a single gang of net.

Walleye from 50 to 200 mm fork length were captured in 1978 using a bottom trawl. The trawl was 19 m long with an 18 m footrope and 1.27 cm mesh in the cod-end. The gear was fished over a distance of 0.4 km at up to eight locations in the bay at monthly intervals from May through September (Fig. 1).

The length and weight were measured on each walleye captured. The state of sexual maturity was recorded, and a scale sample was retained for later age determination. The stomach contents were examined, and the species and length of each fish eaten were recorded, if possible. The lengths of chironomid larvae and pupae were also recorded, and the numbers of *Leptodora kindtii* in YOY were counted. Lengths of chironomids were converted to weights using a L–W regression developed by Johnson and Brinkhurst (1971).

Simulation of Walleye Growth

The energy content of walleye carcass derived from analysis of eight fish in May 1972 was 19172 $\mathrm{J \cdot g}$ dry weight^{-1} (Kelso 1972). Percent water content for a variety of fish species ranged from 74.6 to 54.4% (Cummins and Wuycheck 1971). Using these values, the energy content of walleye ranged from 4870 to 8742 $\mathrm{J \cdot g}$ wet weight^{-1}. Minton and McLean (1982) measured the energy content of sauger (*Stizostedion canadense*) at monthly intervals over the entire year and give values of 5900 $\mathrm{J \cdot g^{-1}}$ for carcass and 17 600 $\mathrm{J \cdot g^{-1}}$ for gonadal tissue. These latter values were used in the present study, primarily because they represent a mean for the whole year. In addition, both species show similar growth characteristics and eat similar prey (Scott and Crossman 1973).

A growth curve based on the von Bertalanffy equation was calculated for female walleye of the 1978 year-class. Estimates of somatic growth and the stored energy of reproductive tissue were made using a method developed by Ware (1980). This required data on gonadal weight and body weight, plus size at sexual maturity, egg weight, and fecundity. Measures of these parameters were made by Payne (1963) on walleye of the Bay of Quinte in the 1958–63 period. Since walleye growth rate and population density in the late 1970s and early 1980s are similar to those in the 1958–63 period, the values determined by Payne (1963) were used for the 1978 year-class.

Estimates of Daily Ration

The daily ration of both YOY and adults was estimated from the stomach contents of fish captured by both trawl and gillnet. Trawling was effective in taking YOY and juveniles, but not adults. Gillnets captured juveniles and adults, but the fact that digestion would continue after capture makes this gear less desirable for estimating daily ration. The probability of capturing a walleye soon after it has eaten and before complete digestion of its meal occurred was not measured. Gillnet sets of 3, 6, and 12 h duration captured the same proportion of walleye that had entire fish, completely digested fish (spines remaining), and chyme in their stomachs. The assumption was made, therefore, that the mean contents of all fish captured in any gear was an estimate of the mean amount of food in the stomach over a 24-h period. Since adult walleye show some degree of feeding activity over the 24-h period (Swenson and Smith 1973), this assumption is not unfounded.

An equation relating time in hours (y) to 90% evacuation of stomach contents and the ambient temperature (T) for walleye and sauger was developed by Minton and McLean (1982):

$$(1) \qquad y = 107.85e^{-0.1046T}$$

The equation developed by Elliott and Persson (1978) to estimate daily food consumption (Co) is given by

$$(2) \qquad \mathrm{Co} = 24\bar{S}\alpha$$

where $\bar{S}$ is the mean amount of food in the stomach over a 24-h period and α is the exponential rate of gastric evacuation.

A value of 90% evacuation was used because Minton and McLean (1982) stated that the final or residual phase of the digestion of bony tissue is highly variable. The equation to calculate α is

TABLE 1. Values for prey weight, predator weight, and energy content used in the bioenergetics model.

	Wet weight, g mean or range		Energy content, $J \cdot g^{-1}$
Leptodora kindtii	0.000414[a]		917[b]
Chironomid larvae and pupae	0.01[c]		2976[b]
Alewife	0.5–40[d]	Jan.	7204[e]
		Feb.	6254
		Mar.	5253
		Apr.–June	5304
		July	5700
		Aug.	6053
		Sept.	6455
		Oct.	7702
		Nov.	9105
		Dec.	8205
Rainbow smelt	0.5–35[d]		5700[b]
White perch	0.5–40[d]		5700[b]
Yellow perch	0.5–40[d]		5700[b]
Walleye	0.5–1560[d]		5900[b] – 6730 (using energy content of gonadal tissue of 17600 $J \cdot g^{-1}$)[f]

[a] Cummins et al. (1969).
[b] Cummins and Wuycheck (1971).
[c] Mean of five species, Johnson and Brinkhurst (1971).
[d] Field data, Bay of Quinte.
[e] Stewart et al. (1983).
[f] Minton and McLean (1982).

(3) $$\alpha = \frac{\ln 90}{y}$$, for any stated temperature.

Bioenergetics Model

The model used was originally described by Kitchell et al. (1974) and modified to apply to walleye (Kitchell et al. 1977). Further modifications have been made to the original model by Stewart et al. (1981, 1983) so that variations in energy content ($J \cdot g^{-1}$) of both predator and prey are considered and a calculation of prey consumption by a predator population can be made.

In its present form, the model was written in Apple Pascal by Steve Hewett and John Lyons, Center for Limnology, University of Wisconsin, Madison, WI, USA. The data required for the computations are daily temperature, daily composition of the predator diet as a fraction of each prey item by weight, the energy content of each prey item on a monthly basis, the average weight before digestion of each prey type, and the energy content of walleye. Values used in the model for the energy content of prey and walleye are given in Table 1.

Predicted body weights for each month May through August derived from the model simulations were compared to the observed body weights. If predicted weights were within 2 SE of the mean observed weights, the model was considered to describe walleye growth. Rice and Cochran (1984) used a similar criterion in their simulation of largemouth bass, ***Micropterus salmoides***, growth and found no significant lack of fit using this criterion.

The growing season for walleye in the Bay of Quinte is approximately 4 months long, from early June through September (Payne 1963). A similar growing period (May–Sept.) was reported for walleye in Oneida Lake (Forney 1977). This period in the Bay of Quinte coincides generally with the timing of temperatures at 15°C and greater. The range from 1978 through 1983 of 15°C in the upper bay was from May 12 to October 12 for the longest period, and May 24 to September 29 for the shortest period.

Walleye ceased body growth, except for gonadal development, by mid-October (Payne 1963) so that body weights were maintained from mid-October to the following May at the May value. No estimate of standard error could be made for these months.

The daily ration was adjusted in the model by calculations of a value for the proportionality constant, *P*, which determines the actual fraction of the maximum daily ration eaten that adequately describes the walleye growth. Values for *P* assume that feeding is a function of temperature and predator weight (Rice and Cochran 1984) provided prey availability remains constant.

Walleye growth could only be predicted by determining *P* values over several time periods within any one year. In general, one value was adequate for the period January to mid-May. Between mid-May and mid-August one value was adequate, i.e. predicted weights within 2 SE of the observed mean weights, in some but not all years. August to December weight estimates were described by one value for *P*.

Other constants used in the model were identical to those given by Kitchell et al. (1977) with values different for YOY and juvenile–adults. The value for regression intercept describing the proportion of consumed food egested depends upon the invertebrate–vertebrate mix in the diet. This value was calculated using the proportion of invertebrates in the diet of YOY walleye and reaching a 95% vertebrate–5% invertebrate diet by September 15. This same proportion was the average observed for all older ages and was used in the model.

Three levels of annual instantaneous mortality rates and initial population were used: one used a constant annual mortality (*Z*) from June 1, 1978 through 1983, and equalled 0.769, a value close to one determined from spring and fall trapnets 1980–84 (Dentry et al. 1985), and population of 250 000 age 3 in August 1981. The next two simulations began with the same age 3 population but extrapolated back to June 15, 1978, with varied annual values for *Z* from 2.30 at age 0 to 0.769 at age 5, and *Z* from 1.488 at age 0 to 0.769 at age 5.

Weight of prey fish was dependent upon walleye size in that YOY walleye ate fish from 0.5 in June to 2 g in September. For age 1 walleye this range gradually increased over the summer from 2 to 40 g.

Energy content of walleye increased as a result of gonadal development in age 3 and older fish. The value was calculated from (1) the percent maturity and female fork length from Payne's (1963) data for Bay of Quinte walleye:

(4) $$FM = -3.85 + 0.0098L \qquad R^2 = 95.9\%$$

where *FM* is the fraction of females mature and *L* is fork length (mm) and (2) the relationship between maximum ovary weight (Mar.–Apr.) and body weight:

(5) $$OW = 0.25BW - 206.62 \qquad R^2 = 93.5\%$$

where *OW* is ovary weight (g) and *BW* is total body weight including ovaries (g).

Monthly increments to female gonadal tissue were calculated from a graph relating gonadal biomass and months from

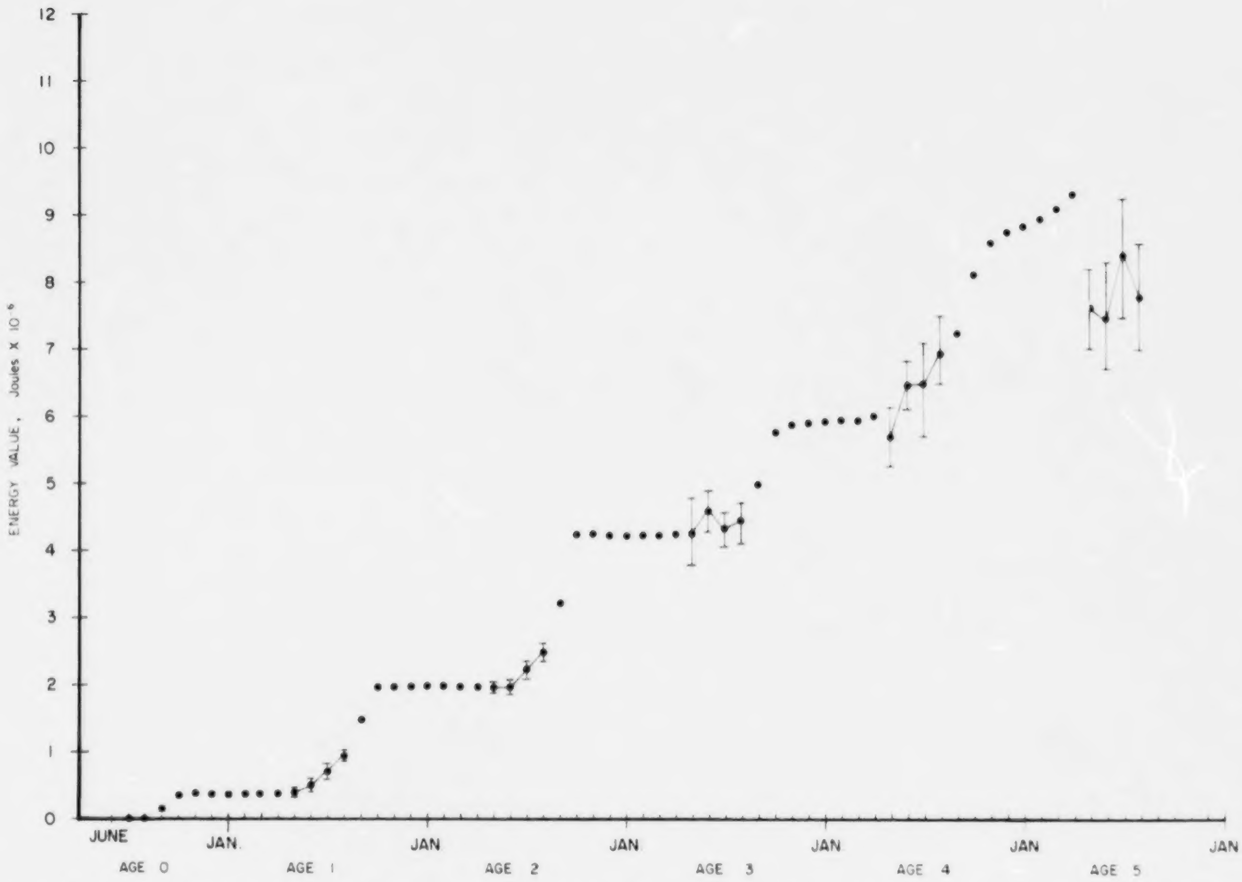

FIG. 2. Energy values ± 2 SE calculated from observed weights for May–August of the 1978 year-class of walleye with extrapolated values for September–April together with energy values associated with female gonadal tissue. Spawning set to occur on April 15.

October to April (Payne 1963). The increments were calculated for female gonadal tissue only. This would tend to overestimate the energy requirement for age 3, 4, and 5 walleye. Male gonadal tissue at maximum accounts for 5% of the body weight, while that for females reaches 19% of the body weight (Payne 1963).

Daily temperatures were taken from records at the Belleville Public Utilities Commission filtration plant where the temperature of incoming water from a depth of 4 m in mid-channel of the bay is measured between 8 and 9 a.m. each day.

The proportion of different prey items in the walleye diet was determined from stomach analyses of walleye from YOY to adults. These data were entered into the model on a daily basis and were altered as proportions of diet items changed.

A downward adjustment of the populations of age 4 and age 5 walleye in the bay from May 16 to August 31 was made, since Payne (1963) reported that 50% of age 4 and 70% of age 5 walleye leave the bay for open Lake Ontario and are resident there for that time.

Results

Fish Growth

Effect of sex and fishing location

The effect of different locations in the bay on walleye growth was examined. Data on walleye captured in the 1978–84 period did not show a consistent difference in length at age between the upper bay (Trenton to Deseronto) and the lower bay (Hay Bay to Conway). Mean values ± 2 SE overlapped in all but ages 1 and 5 for female walleye and in all but age 4 for male walleye. In later examination, therefore, walleye from all locations were combined.

The 1978 year-class showed sex related growth difference only at age 3 and 4 when females were significantly larger than males. The difference was only 21 and 24 mm, respectively. Weight differences were more pronounced. Age 3 females were 140 g heavier than males and age 4 females were 240.5 g heavier than males. However, differences at age 1, 2, 5, and 6 were not significant. In view of the relatively few walleye involved in the analysis, it was decided that males and females would be combined to form a single group at each age.

Energy value of sampled walleye

Values for mean monthly weight of the 1978 walleye year-class age 1 to 5 in the months May–August were obtained from sampled walleye. Estimates of gonadal weight were made using the equation derived for fraction of females mature against fork length. This fraction and the actual gonadal biomass were added as a monthly increment from October to April. Since walleye spawn in April, the loss of gonadal tissue occurred as a step function on April 15. The mean weight recorded in May is for somatic tissue only (Fig. 2).

The weight values and estimates were converted to joules

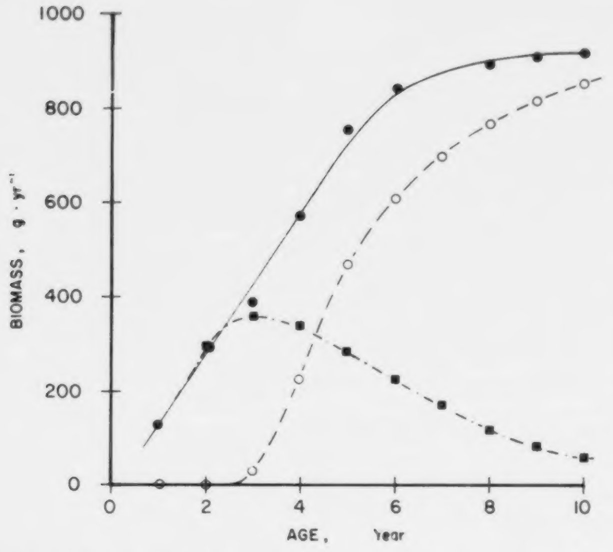

FIG. 3. Calculated weight increments at age for a female walleye of the 1978 year-class showing surplus energy (●), which is the sum of the somatic growth (■) and reproductive effort (○), during the first 10 yr of life.

using 5900 J·g⁻¹ for somatic tissue and 17 600 J·g⁻¹ for gonadal tissue. Since growth of somatic tissue ends in October (Payne 1963), the values between October and May were held constant. There is, however, the possibility that energy content decreases over winter. Examination of walleye caught in October–December showed evidence of fat accumulation in the abdominal mesenteries. This storage of fat with its high energy content (32 200 J·g⁻¹, Minton and McLean 1982) would be depleted over winter for routine metabolism and gonadal development. Since no measurements of fat content were made, it was not possible to estimate the energy value of this material. This would reduce the energy value calculated for the late fall and winter.

The mean energy value per walleye increased with age as did the variance about the mean (Fig. 2). The values reported here compare closely to those reported by Minton and McLean (1982) for sauger from age 0 to age 3 (0.938×10^6 to 5.102×10^6 J) and show that their sauger grew, in weight, at about the same rate as did Bay of Quinte walleye.

Energy value from Ware (1980) model

Ware (1980) developed a model to calculate surplus energy, which he defined as the net energy left after standard metabolism and swimming activity have been accounted for. It represents both somatic growth and the stored energy of gonadal tissue which is released at a specific time.

Several equations are necessary to estimate the annual surplus energy. For the length–weight regression, data were obtained from walleye taken in trapnets (Fig. 1) in the 1969–81 period:

$$\text{(6)} \qquad \log W = -5.336 + 3.155 \log L \qquad R^2 = 98.0\%$$

where W is body weight (g) and L is fork length (mm).

The energy related to reproductive products was calculated for females only. Fecundity was measured on Bay of Quinte walleye by Payne (1963) and yielded the following equation:

$$\text{(7)} \qquad F = 3.76\, W^{1.368} \qquad R^2 = 97.1\%$$

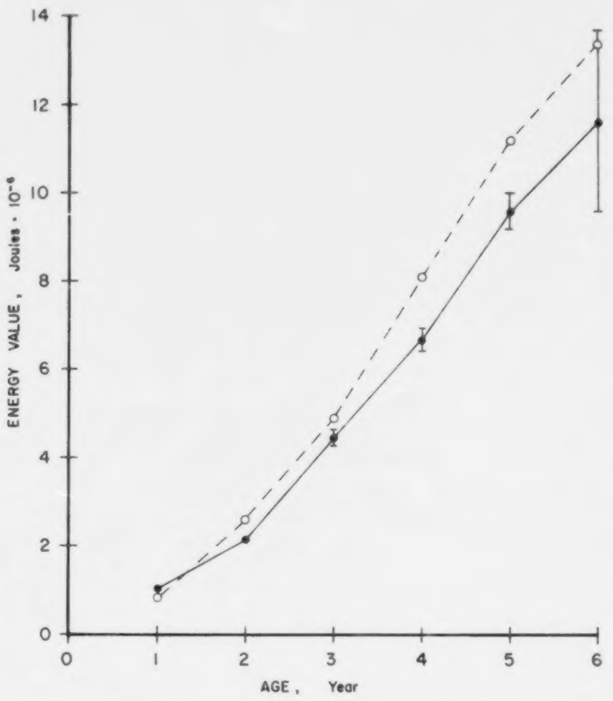

FIG. 4. Energy value per average female walleye of the 1978 year-class derived by Ware's (1980) formula (○) and calculated from observed growth ± 2 SE (●).

where F is number of eggs.

The weight of an individual egg was derived from weights of 11 mature ovaries and an estimate of egg numbers in each ovary. The mean value thus obtained was 0.00216 g.

A growth curve was developed based on the von Bertalanffy equation using female length at age for the 1978 year-class. Data for ages 1 to 6 only were available:

$$\text{(8)} \qquad L_t = 569\,(1 - e^{-0.365(t\,+\,0.472)}).$$

Calculation of reproductive effort (ΔR, g·yr⁻¹) was made using Ware's (1980) equation:

$$\text{(9)} \qquad \Delta R = C\theta f W^{\phi}$$

where C and ϕ are constants obtained from the fecundity equation

$$F = CW^{\phi} \qquad (C = 3.76,\ \phi = 1.368),$$

θ is the weight of an egg (0.00216 g), f is a dimensionless constant that adjusts for the higher energy content of gonadal tissue. Values for sauger (Minton and McLean 1982) were used (f = 17600 J·g⁻¹/5900 J·g⁻¹ = 2.98).

Substituting these values in the above equation for reproductive effort yields

$$\text{(10)} \qquad \Delta R = 0.0242\, W^{1.368}.$$

From these data a schedule relating age, mean body weight, and surplus energy was developed for the 1978 year-class of female walleye. The regression calculated from these data was

$$\text{(11)} \qquad \Delta S = 12.46\, \overline{W}^{0.562} \qquad R^2 = 99\%$$

where ΔS is surplus energy (g·yr⁻¹) and $\overline{W}$ is annual mean weight (g).

TABLE 2. Energy content of food items in stomachs of small walleye (2.0–100.0 g), 1978–79, as percentage of total. Percent occurrence of item in samples given in parentheses. An estimate of daily ration is also shown.

	Walleye weight class, g						
	2.0–4.9	5.0–9.9	10.0–14.9	15.0–29.9	30.0–49.9	50.0–74.9	75.0–99.9
Number of walleye	28	33	24	50	54	61	26
Number of empty stomachs	3	1	6	13	8	14	4
Mean energy value of contents, $J \cdot g^{-1}$ predator	14.4	28.5	19.6	48.0	41.5	26.5	33.9
Leptodora kindtii	23.9	13.3	5.6	<.1	<.1	<.1	0
	(82.1)	(63.6)	(16.7)	(6.0)	(1.9)	(1.6)	
Chironomid larvae	4.5	0.4	5.1	2.8	1.7	0.3	0.4
	(10.6)	(3.0)	(12.5)	(28.0)	(22.2)	(19.7)	(23.1)
Chironomid pupae	0	2.1	4.6	5.7	7.8	4.9	0.4
		(9.1)	(16.6)	(36.0)	(33.3)	(14.8)	(23.1)
Fish	71.6	84.0	84.7	91.4	90.3	94.8	99.2
	(14.3)	(30.3)	(45.8)	(30.0)	(50.0)	(65.6)	(65.4)
Estimated daily ration, $J \cdot g^{-1} \cdot d^{-1}$	197.1	390.1	241.6	532.9	336.7	174.4	376.4

The derived values for surplus energy, reproductive effort, and somatic growth are shown in Fig. 3, and illustrate the fact that while surplus energy rises continually until maximum size is reached, somatic growth increments reach a maximum at an early age and then decrease. The difference between surplus energy and energy for somatic growth represents reproductive effort. This rises quickly once walleye mature and, among older females, accounts for the major portion of surplus energy. The values for energy have been given in terms of weight but can be easily converted to energy units, assuming $5900 \ J \cdot g^{-1}$, since the higher energy content of gonadal tissue has already been accounted for in the constant f (2.98).

The mean energy value per walleye for each age derived from Ware's (1980) model is shown in Fig. 4 together with the calculated values from observed walleye growth. No error estimate was computed for the Ware formula but data derived from that model were, except for age 1, all greater than those from the observed group.

Stomach Contents of Walleye and Estimated Daily Ration

YOY and juveniles

YOY walleye from 2 to 15 g in weight consumed large numbers of *Leptodora kindtii* (Table 2). A mean of 37.5 *Leptodora* were found in each of 28 walleye in the 2.0–4.9 g size class. There is strong evidence that YOY walleye select *Leptodora* as food since the mean concentration of this zooplankton on a seasonal basis was found to range between 50 and $475 \cdot m^{-3}$ (Cooley 1984), while that for smaller cladocerans such as *Eubosmina coregoni* averaged $43\,000 \cdot m^{-3}$ and for *Bosmina longirostris* averaged $56\,000 \cdot m^{-3}$ in the May–October period (J. Cooley, GLFRB, Burlington, Ont., pers. comm.). In spite of this numerical abundance of small cladocerans, none was found in the stomachs of walleye in the size range studied here.

Walleye over 15 g in weight ate few *Leptodora*, but the proportion of fish in the diet steadily increased to reach 99% by the time walleye were 75 g in weight. Chironomid larvae and pupae were the only other items in YOY diet that were consistently present. They formed up to 10% of the energy content of the stomach contents of walleye less than 50 g. Chironomid pupae were often more commonly found than were the larvae. These were probably taken as the pupae were rising to the water surface.

The mean energy value of the stomach contents remained relatively constant between 14.4 and $48.0 \ J \cdot g^{-1}$ and was apparently unrelated to predator size.

Estimates of the daily ration of YOY and juvenile walleye of various size ranges were made using the method outlined by Elliott and Persson (1978) and from trawl captured fish. Daily ration ranged between 174.4 and $532.9 \ J \cdot g^{-1} \cdot d^{-1}$ (Table 2). The lowest value was recorded for YOY in September when mean water temperature was 18°C although values for months when temperatures ranged from 20 to 25°C were as low as $197.1 \ J \cdot g^{-1} \cdot d^{-1}$.

Adults

A total of 1344 walleye stomachs were examined from gillnet captured fish in the May–September period, 1977–84 (Table 3). The energy value of those identifiable prey items are shown in Table 3 for walleye size ranges from 50 to 1600 g. Alewife (*Alosa pseudoharengus*) form the major diet item with rainbow smelt (*Osmerus mordax*), yellow perch (*Perca flavescens*), and white perch following in that order. Prey included in the other classification included gizzard shad (*Dorosoma cepedianum*), johnny darter (*Etheostoma nigrum*), sculpin (*Cottus* sp.), and brook stickleback (*Culaea inconstans*). Many walleye examined contained digested portions and spinal columns of fish that were not identifiable. These were not included in the survey.

The energy value of the stomach contents generally rose among the large walleye. A shift from yellow perch and rainbow smelt in May to alewife in June and later months can also be seen in the data. This reflects the lower abundance of alewife in the bay in May compared to later months (Hurley 1986).

The range of values for the mean energy of the stomach contents per gram walleye remained essentially the same for all size classes examined. There did not appear to be a consistent difference related to months between May and September, although the highly variable nature of the data makes it difficult to draw conclusions.

Estimates of the daily ration for adults were highly variable across months and walleye size classes (Table 3). The range was between 13.7 and $1672.4 \ J \cdot g^{-1} \cdot d^{-1}$. The lowest average daily consumption occurred in May while other months had generally similar consumption rates ($500–700 \ J \cdot g^{-1} \cdot d^{-1}$).

TABLE 3. Mean monthly energy value of stomach contents of walleye of various weight classes in the Bay of Quinte 1977–84. Mean monthly temperatures at Belleville Filtration Plant ± 1 SD are also given.

			Energy value of stomach contents, $J \cdot stomach^{-1}$							
Month	Walleye weight class, g	No.	Alewife	Rainbow smelt	White perch	Yellow perch	Other	Total	Mean, $J \cdot g^{-1}$	Est. mean daily ration, $J \cdot g^{-1} \cdot d^{-1}$
May	50–150	34	0	1792	0	0	0	1792	17.9	83.5
	300–400	104	0	1330	0	925	0	2255	6.4	29.9
$T = 14.7 \pm 2.8°$	600–800	30	8728	14179	0	0	0	22907	32.7	152.6
	900–1300	60	6564	7786	0	20795	0	35145	32.0	149.3
	1300–1600	24	18626	2760	0	16660	0	38046	26.2	122.2
June	50–150	46	865	0	0	0	0	865	8.7	72.4
	300–400	89	16793	8165	12	0	0	24970	71.3	593.7
$T = 20.3 \pm 2.0°$	600–800	87	66213	762	0	3565	1285	71825	102.6	854.4
	900–1300	155	61786	3533	0	963	0	66282	60.3	502.1
	1300–1600	115	80756	0	0	385	0	81141	56.0	466.3
July	50–150	23	2079	1846	0	2399	0	6324	63.2	756.6
	300–400	60	13180	35725	0	0	0	48905	139.7	1672.4
$T = 23.7 \pm 1.4°$	600–800	57	1428	0	0	0	0	1428	2.0	23.9
	900–1300	48	16444	0	0	0	0	16444	14.9	178.4
	1300–1600	14	38084	0	0	0	0	38084	26.3	314.8
Aug.	50–150	98	760	5561	6048	0	356	12725	127.3	1455.4
	300–400	98	2240	2258	264	332	331	5425	15.5	177.2
$T = 23.3 \pm 3.2°$	600–800	63	30250	2738	0	0	0	33988	48.6	555.6
	900–1300	58	14859	0	0	0	0	14859	13.5	154.3
	1300–1600	34	1757	0	0	0	0	1757	1.2	13.7
Sept.	50–150	0	—	—	—	—	—	—	—	—
	300–400	28	4556	22323	0	0	4094	30973	88.5	673.6
$T = 19.4 \pm 2.4°$	600–800	4	0	0	0	0	111247	111247	158.9	1209.4
	900–1300	15	33137	0	0	0	6909	40046	36.4	277.0
	1300–1600	0	—	—	—	—	—	—	—	—

TABLE 4. Correlation of prey fork length on walleye fork length. Significance at 0.01 level indicated by **.

	Alewife	Rainbow smelt	Yellow perch
Number of pairs	459	131	65
Size range of prey, mm	12–200	12–200	25–170
r	0.284**	0.341**	0.790**

Effect of Predator–Prey Size Relationships

There was a highly significant correlation between walleye length and the length of their prey ($P < 0.01$) for alewife, rainbow smelt, and yellow perch (Table 4). The number of pairs of comparisons in the case of white perch (20) were insufficient to show a positive relationship. The range of sizes of alewife eaten by larger walleye (400–600 mm) was between 12 and 200 mm, with the majority of prey in the 125–175 mm range. Similarly, rainbow smelt over a large size range were eaten, but the majority were in the 50–150 mm range.

Bioenergetics Model

The results of the simulation for the three scenarios for initial walleye numbers and annual instantaneous mortality rates are given in Table 5. It is proposed that the values given for scenario 3 are minimal since assuming constant mortality level from age 0 is probably not biologically valid. It is proposed, therefore, that scenarios 1 and 2 are more likely.

Alewife form the major component in the simulated diet because the value for this prey item was set according to the observed diet composition at the various ages. It was assumed that alewife were a major diet item for YOY walleye even though the fish remains were largely unidentifiable in this group.

The consumption of both white perch and yellow perch appears high in comparison to the values given for stomach contents in Table 3. However, it was assumed that consumption of these species would increase in October–April when alewife numbers were lower. Similarly, rainbow smelt abundance is high in the middle and lower bay and not in the upper bay. Therefore, the proportion of this species in the diet was averaged over all locations. The greater consumption of yellow perch in May and June as seen in Table 3, when alewife were less available, illustrates the changing walleye diet pattern with prey abundance.

The summed consumption for each prey item over all years would simulate the effect of a walleye population in the bay for one year. Total populations for all age groups 0 through 5 on June 15 was calculated to be for scenario 1, 3.56×10^7, for scenario 2, 1.89×10^7, and for scenario 3, 4.97×10^6 walleye.

Daily Energy Consumption

The model produced estimates for the daily ration on any set day using the input variables for temperature, walleye growth, and diet composition. Monthly values for age 0 walleye are recorded in Table 6 with typical values for late winter, early and late summer for other ages. Maximum daily intake per gram of walleye occurred at age 0 and decreased rapidly thereafter. Lowest values for daily consumption occurred in winter months from December through March; highest values were recorded in June to September.

The high estimated daily consumption of age 0 walleye is the

TABLE 5. Calculated annual prey consumption from bioenergetics model for the 1978 year-class of walleye in the Bay of Quinte for three different initial (June 15, 1978) population sizes and natural mortality rates.

Age	Estimated initial population[a]	Instantaneous natural mortality rate, Z	Prey consumed, t·yr⁻¹						
			Leptodora kindtii	Chironomid larvae	Chironomid pupae	Alewife	Rainbow smelt	White perch	Yellow perch
Scenario 1									
0	3.0×10^7	2.303	122.3	88.3	60.3	1376.8	242.8	244.1	294.0
1	8.5×10^6	1.568	0	27.9	118.8	1830.5	174.5	335.3	446.5
2	1.8×10^6	1.151	0	16.8	56.7	894.0	90.2	170.3	241.0
3	5.6×10^5	1.151	0	10.0	21.4	359.8	41.3	75.6	119.3
4	1.8×10^5	0.769	0	3.9	7.9	133.8	15.7	29.3	44.9
5	8.1×10^4	0.769	0	2.3	3.3	60.8	8.2	15.1	24.0
Σ			122.3	149.2	268.4	4655.7	572.7	869.7	1169.7
Scenario 2									
0	1.4×10^7	1.488	61.7	50.7	33.1	789.8	137.5	138.5	163.6
1	6.2×10^6	1.255	0	23.5	105.4	1616.9	152.5	295.0	385.4
2	1.8×10^6	1.151	0	16.8	56.7	894.0	90.2	170.3	241.0
3	5.6×10^5	1.151	0	10.0	21.4	359.8	41.3	75.6	119.3
4	1.8×10^5	0.769	0	3.9	7.9	133.8	15.7	29.3	44.9
5	8.1×10^4	0.769	0	2.3	3.3	60.8	8.2	15.1	24.0
Σ			61.7	107.2	227.8	3855.1	445.4	723.8	978.2
Scenario 3									
0	2.8×10^6	0.769	12.7	11.8	7.4	183.6	31.6	31.9	37.1
1	1.8×10^6	0.769	0	8.5	40.8	623.1	57.9	113.4	144.0
2	8.2×10^5	0.769	0	9.1	33.6	525.2	51.8	98.9	135.7
3	3.8×10^5	0.769	0	7.8	18.5	305.3	34.1	63.2	96.8
4	1.8×10^5	0.769	0	3.9	7.9	133.8	15.7	29.3	44.9
5	8.1×10^4	0.769	0	2.3	3.3	60.8	8.2	15.1	24.0
Σ			12.7	43.4	111.5	1831.8	199.3	351.8	482.5

[a] Population estimate at January 1 each year and set for age 0 on June 15.

TABLE 6. Daily consumption of 1978 year-class of walleye calculated from bioenergetics model.

Age	Day	Daily food consumption	
		mg·g⁻¹	J·g⁻¹
0	July 15	135.2	577.1
	Aug. 15	93.1	484.7
	Sept. 15	49.7	294.9
	Oct. 15	25.4	174.4
	Nov. 15	5.6	43.2
	Dec. 31	3.1	22.3
1	Mar. 15	3.3	17.8
	June 15	39.4	208.4
	Sept. 15	29.4	179.1
2	Mar 15	2.4	13.2
	June 15	10.2	53.9
	Sept. 15	26.9	164.1
3	Mar. 15	2.2	11.9
	June 15	13.0	68.7
	Sept. 15	17.1	104.4
4	Mar. 15	1.8	9.8
	June 15	14.2	75.1
	Sept. 15	13.0	68.7
5	Mar. 15	3.1	17.0
	June 15	10.8	55.0
	Sept. 15	14.2	86.5

consequence of the rapid growth of these fish — from a mean of 0.5 g in mid-June to 24.4 g in mid-August. The growth model traces this rapid growth only because the ratio of actual food consumption to maximum possible consumption (*P*) is 0.82 and the diet consists of from 70 to 90% fish (Table 2) which are relatively energy rich (5300–9100 J·g⁻¹) compared to *Leptodora* (917 J·g⁻¹) and chironomids (3000 J·g⁻¹).

To test the hypothesis that piscivorous behaviour among walleye is energetically necessary, a simulation of age 0 growth was attempted where the diet was assumed to be 80–90% invertebrates and only 10–20% fish. With this constraint even maximum daily ration ($P = 1.0$) would not permit the observed growth to occur. It appears, therefore, that the conversion from invertebrate to fish diet was necessary at a small size in walleye in order to maintain their growth rate.

Daily Specific Growth Rate and Conversion Efficiency

The simulation of walleye growth and daily ration provided values for daily specific growth rate (g·g⁻¹·d⁻¹) and gross conversion efficiency which measures the proportion of daily ration that is converted to fish biomass. Specific growth rates and conversion efficiencies (Table 7) were high among age 0 and age 1 walleye compared to values of 20.4–29.4% quoted by Minton and McLean (1982) for sauger of the same age. Values for older walleye, however, are generally similar to those quoted by Swenson and Smith (1973) for walleye, 21.2–30.1%.

The high growth rate and gross conversion efficiency exhibited by age 0 fish resulted from the higher rations ($P = 0.82$) of these fish which tended to produce a better conversion efficiency (Stewart et al. 1983). This occurred despite the fact that the proportion of invertebrates, of which about 10% of their weight is indigestible (Stewart et al. 1983) compared to only 2–3% for fish (Kelso 1972), in YOY diets was relatively large.

TABLE 7. Specific growth rates and conversion efficiencies of the 1978 walleye year-class calculated from the bioenergetics model on specific dates and measured temperatures.

Age	Date	T, °C	Specific growth rate, $g \cdot g^{-1} \cdot d^{-1}$	Gross conversion efficiency, %
	1978			
0	July 15	23.5	0.068	50.4
	Aug. 15	23.5	0.045	48.8
	Sept. 15	18.5	0.024	48.6
	Oct. 15	12.0	0.012	48.6
	Nov. 15–Dec. 31	8.0–1.0	0	0
	1979			
1	Jan. 1–May 15	1.0–17.5	0	0
	June 15	20.5	0.016	40.0
	July 15	23.5	0.012	32.8
	Aug. 15	21.0	0.013	38.1
	Sept. 15	19.5	0.012	39.2
	Oct. 15	11.0	0.006	43.1
	Nov. 15–Dec. 31	6.0–1.0	0	0
	1980			
2	Jan. 1–June 15	1.5–18.0	0	0
	July 15	23.0	0.005	23.3
	Aug. 15	25.5	<0.001	1.3
	Sept. 15	19.0	0.011	41.0
	Oct. 15	12.0	0.006	44.0
	Nov. 15–Dec. 31	4.5–1.5	0	0
	1981			
3	Jan. 1–May 15	1.0–13.5	0	0
	June 15	20.0	0.002	13.4
	July 15	26.0	0	0
	Aug. 15	23.0	<0.001	1.1
	Sept. 15	19.5	0.005	29.4
	Oct. 15	11.0	0.003	34.2
	Nov. 15–Dec. 31	6.0–1.5	0	0
	1982			
4	Jan. 1–May 15	1.5–16.0	0	0
	June 15	20.0	0.003	21.3
	July 15	23.5	0.001	10.2
	Aug. 15	22.0	0.002	16.5
	Sept. 15	19.0	0.003	22.2
	Oct. 15	14.0	0.002	25.9
	Nov. 15	6.5	<0.001	4.4
	Dec. 15	1.5	<0.001	3.9
	1983			
5	Jan. 15	1.0	0.001	21.3
	Feb. 15	1.0	0.001	21.3
	Mar. 15	3.5	0.001	21.4
	Apr. 15	8.0	0.001	21.0
	May 15	13.5	0	0
	June 15	19.5	0.001	11.9
	July 15	23.5	0	0
	Aug. 15	22.0	0.001	5.9
	Sept. 15	22.0	0.003	18.0
	Oct. 15	13.5	0.003	27.6
	Nov. 15	5.0	0.001	29.5
	Dec. 15	1.5	0.001	29.7

This would argue that conversion efficiency should be less in YOY fish compared to the adults.

TABLE 8. Calculated production of invertebrate prey of walleye in the Bay of Quinte.

Leptodora kindtii,[a] $t \cdot mo^{-1}$	Chironomids[b] (larvae and pupae), $t \cdot yr^{-1}$
85.9 (June)	12950
102.2 (July)	
217.1 (Aug.)	

[a] Calculated using 200 individuals$\cdot m^{-3}$ (Cooley 1984), P/B: June 2.95, July 3.51, August 7.46 and individual wet weight of 0.414 mg (Cummins et al. 1969), and assuming one-half the bay volume between Trenton and Glenora of 7.03 × $10^8 m^3$ produces *Leptodora*.

[b] Based on Johnson and Brinkhurst (1971) data and using a mean production of 139.1 $g \cdot m^{-2} \cdot yr^{-1}$ for 1967–68 and assuming one-half the bay area produces chironomids.

Walleye in the first three years of life tended to lose weight at various times during the period from November to May. Growth began usually in June but halted again in July and sometimes August when temperatures were over 25°C (Table 7). Among age 5 walleye, this cessation in growth occurred when temperatures reached 23.5°C. These values agree closely with those quoted by Hokanson (1977) for temperature preference and growth optima of walleye.

Age 4 and 5 female walleye were modelled in the simulation to show the effect of the growth of gonads on conversion efficiency. Gain in gonad weight occurred even though food consumption was relatively small in winter. This resulted in a 21% conversion efficiency during these months. Spawning occurred on April 16 so the conversion ratio dropped to zero until June.

Estimates of Prey Biomass and Production

Calculation of production of invertebrates using data from several sources shows that chironomid production is far greater than that consumed by walleye (Table 8). *Leptodora* production may be insufficient to support the calculated consumption by walleye, because consumption by age 0 walleye is confined mainly to the June–July period when *Leptodora* production is relatively low. However, the variability in both production and standing stock is so large from year-to-year among *Leptodora* (Cooley 1984) that definite conclusions about this predator–prey relationship are difficult to draw.

Table 9 lists values for both biomass and production of the major prey fish species as determined by three methods. The values obtained from the bottom trawl May–September in the 1978–83 period are most likely an underestimate because of the low catchability of the younger age-groups. Production was calculated as 1.5 times biomass. This factor is a mean for a variety of freshwater fishes (1–2.1) quoted by Chapman (1978) as yearly rates. For white perch the factor 1.68, determined by Minns and Hurley (1986), was used.

Values derived from life table calculations for three of the species taken in trapnets set at two locations in the bay (Fig. 1) in 1976–81 are given in row 2 of Table 9. These values are higher than the ones derived from trawling, except for alewife. The effective area of fishing for the 6-ft trapnets is not known, but the values shown do have a correction factor for swimming activity built into them. It could be argued that the effective fishing area may range between 0.1 and 1 ha. Production values were derived from the P/B ratios determined by Christie and Scott (1985) as $1.2 \cdot yr^{-1}$ for alewife, $0.8 \cdot yr^{-1}$ for white perch, and $1.1 \cdot yr^{-1}$ for yellow perch in the upper bay, 1976–81.

The third row of Table 9 contains values obtained by multiplying values in row one by 5.6. The correction factor (5.6) was obtained from data on the population structure and production calculations for white perch (Minns and Hurley 1986). The multiplier these authors used in calculating the population stuc-

TABLE 9. Estimates of biomass and production of major fish prey of walleye in the Bay of Quinte.

	Prey species							
	Alewife		Rainbow smelt		White perch		Yellow perch	
Gear type	*B*, $\mathrm{kg \cdot ha^{-1}}$	*P*, $\mathrm{kg \cdot ha \cdot yr^{-1}}$	*B*, $\mathrm{kg \cdot ha^{-1}}$	*P*, $\mathrm{kg \cdot ha \cdot yr^{-1}}$	*B*, $\mathrm{kg \cdot ha^{-1}}$	*P*, $\mathrm{kg \cdot ha \cdot yr^{-1}}$	*B*, $\mathrm{kg \cdot ha^{-1}}$	*P*, $\mathrm{kg \cdot ha \cdot yr^{-1}}$
Bottom trawl	14.1	21.2	9.2	13.8	6.5	10.9	9.9	14.9
Trapnet[a]	6.6	7.9	—	—	98.6	79.4	30.9	31.3
Bottom trawl (corrected for catchability)[b]	79.0	118.7	51.5	77.3	36.4	61.2	55.4	83.1

[a] Values for trapnet-night were adjusted for fish size and swimming speed but effective area not known, see Christie and Scott (1985) for details.
[b] Mean 1978–83 trawl catch per hectare corrected by catchability factor (5.6).

TABLE 10. Prey species production in the Bay of Quinte, 1978–83, as estimated from bottom trawl drags and corrected for catchability.

	Prey species			
Production, $\mathrm{t \cdot yr^{-1}}$	Alewife	Rainbow smelt	White perch	Yellow perch
Uncorrected	393.4	123.3	165.6	225.3
Multiplied by 5.6 to account for catchability	2203.0	690.5	927.4	1261.7

ture of white perch from August trawl catches was applied to the biomass calculations to adjust for the lower catchability of small white perch.

From these estimates, two values for the annual production of prey species from the area of the bay where the prey were produced were derived (Table 10). Those obtained from the bottom trawl, are undoubtedly much too low because of the failure of the gear to sample adequately the younger age-groups when most of the production is elaborated. The values obtained by the correction from Minns and Hurley (1986) has not been validated for any species except white perch and, therefore, can only be viewed as initial estimates. The value for white perch, however, was derived from a life table analysis of growth, egg production, and mortality, and therefore can be accepted with more certainty.

Assumptions Used in Setting Model Parameters

Several assumptions were made in operating both the bioenergetics model and the surplus energy model.

(1) Water temperatures recorded at the Belleville Filtration Plant adequately describe the thermal regime of the bay.

Water temperature profiles were recorded at monthly intervals at up to nine locations in the bay between Trenton and Indian Point (Fig. 1). Examination of records from 1978 through 1982 showed that between Trenton and Big Bay the water column was homothermous and the temperatures were less than 2°C above or below the Belleville intake temperature from the end of May to the end of October. From Deseronto to Hay Bay some degree of thermal stratification occurred in the deepest water depths at 10 m that were deliberately used in the limnology surveys. Since the mean depth of the upper bay from Trenton to Deseronto is 3.2 m and that of Hay Bay is 1.9 m, it is reasonable to use temperatures at Belleville taken at 4 m to be representative of the bay from Trenton to Hay Bay. Deeper water from Glenora to Amherst Island (mean depth of 23.8 m) plus the periodic influx of colder Lake Ontario water (Freeman and Prinsenberg 1986) makes the use of Belleville temperatures in this area unsuitable. Walleye abundance, however, is generally lower in this deeper portion of the bay (Hurley 1986). Those walleye that may have spent time in these colder waters would not show the same degree of food consumption calculated for that at the higher temperatures. Consumption, daily ration, conversion efficiency would be therefore overstated for these fish.

(2) Instantaneous total mortality rates were held constant throughout the year but do change from YOY to adults.

There are no data available on within year changes in mortality rates but there are data for various age-groups. From July to October 1963, in Oneida Lake, Forney and Houde (1964) quote instantaneous daily rates of 0.011 to 0.014 for age 0 walleye. Forney reported that in the August–October period 1967, the daily instantaneous rate for age 0 walleye was 0.0026 (J. L. Forney, Cornell Biological Field Station, Bridgeport, NY, pers. comm.). The range of these values in annual rates is from 0.95 to 5.11 which covers the range used in two of the three simulations. For adult walleye, annual rates of 0.14 to 1.83 are reported (Colby et al. 1979). The values used in the simulation were within these limits. No attempt was made to differentiate between natural and fishing mortality although fishing mortality is substantial among walleye age 2 and older. Mortality, therefore, was calculated as a total daily instantaneous rate.

(3) Diet composition, proportion of prey items, and stomach fullness were adequately determined by examining walleye captured in bottom trawls and gillnets.

Minton and McLean (1982) examined the possibility that feeding sauger may be more mobile than non-feeding ones and, therefore, be more susceptible to the gillnet resulting in overestimation of the ration. They concluded that this was not so and both feeding and non-feeding sauger were equally liable to capture. Prey density has been correlated with consumption rates in northern lakes (Swenson 1977) so the stomach contents may be used as an indicator of prey availability but would be subject to error if prey preference was an important factor.

(4) Diet composition during times of the year when walleye were not sampled can be assumed from the known distribution of prey.

Movements of alewife, white perch, and rainbow smelt and the distribution of YOY of these species plus their population changes in the years 1978–83 have been described by Hurley (1986). There was no evidence that adult walleye were being highly selective in their prey, so diet composition and prey distribution can reasonably be considered similar.

(5) The von Bertalanffy equation used with the age–length data for females of the 1978 year-class adequately describes the projected growth of this year-class.

The calculated L_∞ of 569 mm for the 1978 year-class matched closely the value for the combined years 1977–84 ($L_\infty = 573$)

but not for walleye taken in spring trapnets in the upper bay in 1959–61. In that case, the value was $L_\infty = 733$, and ages 2 through 14 were available to calculate the equation. The asymptote is sensitive to slight changes in length values for the older age-groups and thus can alter the L_∞ quite easily. However, because the energy value for walleye calculated from Ware's (1980) equation and that estimated from the observed growth were fairly close together, it was concluded that the von Bertalanffy equation does describe growth of the year-class.

Sensitivity of the Bioenergetics Model

Analyses by Kitchell et al. (1977) and Stewart et al. (1983) illustrate the need for adequate tests of the sensitivity of the input parameters to any bioenergetics model. Stewart et al. (1983) stated that the model is generally robust, especially when the consumption is estimated by fitting a known growth curve, as reported in this paper. A major improvement in earlier versions of this model was made when the energy content of both prey and predator as they change with age and season was incorporated. Consideration of gonadal tissue elaboration and loss also improved the applicability of the model.

Rice and Cochran (1984) found that the model indicated little change in fish weight due to variations of 2°C and 50% increases or decreases in swimming speed. The temperature variations of 2°C covered most of the range observed for Belleville Filtration Plant and limnology surveys, especially in the upper bay. Swimming speeds were not measured in the present study. However, because a ± 50% in swimming speed resulted in only a ± 7% change in body mass, it is presumed that this factor is relatively unimportant in causing major alterations in body weight.

The level of walleye activity, however, does result in major changes in total prey consumption. In the model used in this paper the activity level was set at 1.0 for all simulations and represents a resting metabolic rate (Kitchell et al. 1977). When activity was increased by 50% for adult walleye, food consumption increased from between 32.8 and 34.3%. At a 100% increase in activity, food consumption increased from between 64.5 and 67.9%. There was a corresponding decline of about 30% in the conversion efficiency when the activity was increased 50% and a 50% drop in the conversion efficiency when the activity was increased by 100%.

Adult walleye in lentic, turbid environments, such as the Bay of Quinte, presumably would be inactive for most of the day and feed actively at dawn and dusk (Ryder 1977). This behaviour would result in a relatively low activity level, although the value for the ratio of active metabolism/resting metabolism is not known. Stewart et al. (1983) found the ratio for lake trout ranged between 1.4 and 1.9 depending on temperature and fish size. A range of values between 1.0 and 1.5 for walleye for extended periods of time may be reasonably expected.

A major contribution to alterations in body mass is the value used for *P* (proportion of maximum diet eaten). Both Rice and Cochran (1984) and I showed that this value changes during the growing season and must be fitted to monthly growth data to produce a fit that lies within 2 SE of the mean body weight. Gross errors in estimating consumption could occur if a single value for the entire growing season were assumed.

Discussion

Bioenergetics models have recently been used to examine predator–prey relationships in the Great Lakes (Stewart et al. 1983). They can provide estimates of the amount of prey production that is channelled to predator populations (Stewart et al. 1981). Prey population dynamics in the face of large predator populations maintained by hatchery plantings may be unnaturally stressing the production system (Stewart et al. 1981). However, some authors (Eck and Brown 1985) see prey populations fluctuating as the result of both climatic variations and predation pressure.

The Bay of Quinte walleye production depends only upon natural reproduction and, therefore, the predator–prey relationships are not confounded by artificial manipulation of the population. However, plantings of hatchery-raised salmonids in Lake Ontario have averaged 4.9 million per year between 1978 and 1984 (Anonymous 1985). These fish prey upon the same species as do walleye in Lake Ontario and would, therefore, impact on the prey population in the open lake.

The coefficient relating the consumption by walleye to the production of prey exceeds 1.0 in the case of alewife for scenarios 1 and 2 and is 83% for scenario 3. For other fish species, the ratio ranges from 94 to 29%. For invertebrates, the ratio exceeds 1.0 for *Leptodora* in scenario 1 but decreases rapidly to 13% for scenario 3. For chironomids, the ratio does not exceed 3%. These values for the coefficient termed the ecotrophic coefficient or efficiency of hunting (Chapman 1978) show that a major portion of prey production is consumed by walleye. Under these model simulations where the coefficient exceeds 1.0, prey standing stock is being depleted by predation. In the case where activity level is above the minimum used here, the coefficients would become even greater.

Alewives, unlike the other prey species, make extensive migrations into and out of the Bay of Quinte to Lake Ontario. Large numbers of adult alewives enter the bay each year in late May–early June. They tend to congregate, possibly because of continual migration, in the upper bay. They spawn and the offspring remain for a year before leaving the bay to spend a further year in the lake (Hurley and Christie 1977).

A major source of the walleye diet, therefore, comes from the production capabilities of eastern Lake Ontario and not entirely from the Bay of Quinte. The consumption of a large proportion of the annual alewife production, therefore, does not necessarily mean poor alewife recruitment in subsequent years and a steadily declining population. There is evidence, however, that the standing stocks of alewife in the bay have declined in the Trenton to Deseronto area since 1977 and to a lesser extent in the Deseronto to Glenora area although year-to-year variability in their numbers has been high (Hurley 1986). It is possible that this reduction has occurred as the result of the increasing walleye population of the bay since 1977.

The linear relationship between walleye length and prey length described by Parsons (1971) in Lake Erie and Wagner (1972) in Lake Michigan was also evident in the Bay of Quinte. Walleye in the bay ate more alewife and rainbow smelt than yellow perch, which corresponds to Wagner's findings in Lake Michigan (Wagner 1972). This may be a consequence of the abundance of alewife and rainbow smelt in the 30–40 g size range that could be handled by walleye over 300 mm long. This length is reached by the fall for age 1 fish.

Daily food consumption was generally much smaller according to the bioenergetics model than it was by the calculations from stomach content data for all age classes except for YOY (Table 2, 3, and 6). This could be a consequence of the minimal activity level used in the model simulation. This could also mean that the stomach contents of trawl-caught YOY may be a more reliable source of data than the adult gillnet-caught walleye.

The daily food consumption rate according to the bioenergetics model for age 2 and older fish was about one-half the 30 $mg \cdot g^{-1} \cdot d^{-1}$ rate found for walleye in June through September by Swenson and Smith (1976). This difference may represent the increased consumption that would result from increasing the activity level in the model to some point between 1.5 and 2.0. These authors found the rates were relatively constant when prey density was over 400 $mg \cdot m^{-3}$. The mean biomass of the four main prey fish species of walleye in May–September in the 1978–83 period in the Bay of Quinte was approximately 2500 $mg \cdot m^{-3}$. This value exceeds the point where a restriction on prey availability might be considered.

The daily consumption rates, calculated from stomach contents data (Table 3) for all weight classes that here include from age 1 through age 6 walleye, was highly variable within size classes and between months. They tended, however, to be higher than estimates by Swenson and Smith (1976). Minton and McLean (1982) used a model based on the Winberg (1956) balanced energy equation to calculate daily ration for yearling sauger. They found the ration to be 29.2 $J \cdot g^{-1} \cdot d^{-1}$ in mid-March, and it ranged between 46.3 and 247.0 $J \cdot g^{-1} \cdot d^{-1}$ from May 1 to October 1. These values correspond fairly well with those calculated for walleye from the Kitchell model (Table 6).

The migration of 50% of walleye of age 4 fish, 70% age 5 and 80% of older age-groups from the bay to Lake Ontario soon after spawning (Payne 1963) may be a response to the warm water temperatures encountered in the bay during the summer. These fish return to the bay in late summer and early fall (Payne 1963) when water temperatures are dropping. The bioenergetics model predicted zero specific growth rates among walleye from age 2 to age 5 when water temperatures exceeded 23.5°C (Table 7). Similar results were reported by Kitchell et al. (1977) for simulated growth of Lake Erie yellow perch. Here growth ceased in August when temperatures reached 24°C. It appears, therefore, that the response of older walleye in the bay to high temperatures is migration. There does not appear to be a restriction in prey availability and, even so, the prey consumption by walleye younger than age 4 would be much greater than those of age 4 and older (Table 5).

The production of significant numbers of walleye after 1977 has had profound effects on the fish community of the bay. Hurley (1986) discussed the roles of eutrophication changes and climate variations in possibly molding the fish community. In essence, the community now resembles that observed in the late 1950s when piscivore biomass was large, benthivore and planktivore fishes were abundant but did not dominate the fish community, and algae biomass had not reached nuisance levels.

Assigning the specific role of phosphorus reduction in either causing or facilitating the present community structure has proved to be difficult. Some effects of phosphorus reduction were an abrupt decrease (50–60%) in May–October phytoplankton densities, a shortening of the growing period of bloom-forming species, and a community that would better support the aquatic food web (Nicholls et al. 1986). Macrozooplankton composition, however, did not show some of the expected changes as phosphorous and algal density declined — small cladocerans still dominated and "classic" indicators of cultural eutrophication such as *Chydorus sphaericus* remained abundant (Cooley et al. 1986). The increasing walleye numbers and their simulated daily consumption of prey appear to be restricting the stock of alewife and, probably to a lesser extent, stocks of other fish prey. The lower planktivore, i.e. alewife, population should, theoretically, favour the return of larger-sized zooplankton because of a reduction in predation pressure. This relationship is the subject of numerous papers and has recently been summarized by Carpenter and Kitchell (1984).

The results of the simulations presented here appear to place more emphasis on predator–prey interactions than on trophic interactions. This agrees with a similar hypothesis of Christie and Scott (1985) that they stated for the Bay of Quinte. However, the initial reduction in algal biomass that resulted from phosphorus removal may have been the key initiator of the responses observed at higher trophic levels. This relationship perhaps needs to be emphasized to a greater degree than it has been.

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References

ANONYMOUS. 1985. Annual Report of Lake Ontario Unit, Great Lakes Fisheries Section, Bureau of Fisheries to Great Lakes Fishery Commission, March 1985 meeting.

CARPENTER, S. R., AND J. F. KITCHELL. 1984. Plankton community structure and limnetic primary production. Am. Nat. 124: 159–172.

CHAPMAN, D. W. 1978. Production in fish populations, p. 5–25. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

CHRISTIE, W. J., AND K. A. SCOTT. 1985. A comparison of three warmwater fish communities in the Bay of Quinte area of Lake Ontario. File Report, Glenora Fisheries Station, Picton, Ont. K0K 2T0.

COLBY, P. J., R. E. MCNICOL, AND R. A. RYDER. 1979. Synopsis of biological data on the walleye *Stizostedion v. vitreum* (Mitchill 1818). FAO Fisheries Synopsis No. 119. Rome.

COOLEY, J. 1984. Annual Report of Project Quinte for 1983.

COOLEY, J. M., J. E. MOORE, AND W. T. GEILING. 1986. Population dynamics, biomass, and production of the macrozooplankton in the Bay of Quinte during changes in phosphorus loadings, p. 166–176. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

CUMMINS, K. W., R. R. COSTA, R. E. ROWE, G. A. MOSHIRI, R. M. SCANLON, AND R. K. ZAJDEL. 1969. Ecological energetics of a natural population of the predacious zooplankter *Leptodora kindtii* Focke (Cladocera). Oikos 20: 189–223.

CUMMINS, K. W., AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Limnol. No. 18.

DENTRY, W., B. MALONE, AND T. SCHANER. 1985. Status of walleye stocks in eastern Lake Ontario, 1984. 1984 Annual Report Lake Ontario Fisheries Assessment Unit to the Great Lakes Fishery Commission, p. 1–14, March 1985.

ECK, G. W., AND E. H. BROWN, JR. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. Can. J. Fish. Aquat. Sci. 42: 449–454.

ELLIOTT, J. M., AND L. PERSSON. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977–991.

FORNEY, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34: 1812–1820.

FORNEY, J. L., AND E. D. HOUDE. 1964. Studies of conditions influencing year-class strength of walleyes in Oneida Lake. Federal Aid Fish and Wildlife Restoration Project F-17-R-8, Job. 1-B: 29 p.

FREEMAN, N. G., AND S. J. PRINSENBERG. 1986. Exchange flows in the Adolphus Reach/North Channel, p. 27–39. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

HOKANSON, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34: 1524–1550.

HURLEY, D. A. 1986. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C. K. Minns, D. A.

Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Hurley, D. A., and W. J. Christie. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Johnson, M. G., and R. O. Brinkhurst. 1971. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1699–1714.

Kelso, J. R. M. 1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet, and temperature. J. Fish. Res. Board Can. 29: 1181–1192.

Kitchell, J. F., J. F. Koonce, R. V. O'Neill, H. H. Shugart, Jr., J. J. Magnuson, and R. S. Booth. 1974. Model of fish biomass dynamics. Trans. Am. Fish. Soc. 103: 786–798.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1922–1935.

Minns, C. K., and D. A. Hurley. 1986. Population dynamics and production of white perch, *Morone americana*, in the Bay of Quinte, Lake Ontario, p. 166–176. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minton, J. W., and R. B. McLean. 1982. Measurements of growth and consumption of sauger (*Stizostedion canadense*): implication for fish energetics studies. Can. J. Fish. Aquat. Sci. 39: 1396–1403.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions in phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Parsons, J. W. 1971. Selective food preferences of walleye of the 1959 year class in Lake Erie. Trans. Am. Fish. Soc. 100: 474–485.

Payne, N. R. 1963. The life history of the yellow walleye, *Stizostedion vitreum* (Mitchill), in the Bay of Quinte. Univ. Toronto, M.A. thesis, Toronto, Ont.

Rice, J. A., and P. A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65: 732–739.

Ryder, R. A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1481–1491.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751–763.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40: 681–698.

Swenson, W. A. 1977. Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical environmental conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board Can. 34: 1643–1654.

Swenson, W. A., and L. L. Smith, Jr. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30: 1327–1336.

1976. Influence of food competition, predation and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota J. Fish. Res. Board Can. 33: 1946–1954.

Wagner, W. C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. Trans. Am. Fish. Soc. 101: 55–63.

Ware, D. M. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37: 1012–1024.

Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Belorussian Univ., Minsk. 253 p. (Transl. by Fish. Res. Board Can. Transl. Ser. No. 164, 1960).

Effect of Nutrient Reduction on the Diets of Four Fish Species in the Bay of Quinte, Lake Ontario[1]

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Hurley, D. A. 1986. Effect of nutrient reduction on the diets of four fish species in the Bay of Quinte, Lake Ontario, p. 237–246. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

The diet of alewife, *Alosa pseudoharengus*, changed significantly in the years following the reduction of phosphorus inputs in the Bay of Quinte. Although there were some diet changes among three other fish species examined, they were generally not significant. Copepods formed a larger proportion of the diets of alewife, rainbow smelt, *Osmerus mordax*, and white perch, *Morone americana*, after phosphorus reduction. Fish that ate macrozooplankton showed strong preference for the larger species and avoided smaller species as predicted by optimal foraging theory. Diet overlap was evident between white perch and yellow perch, *Perca flavescens*, only in the lower portion of the Bay of Quinte. Inter- and intraspecific competition may explain changes observed in the growth rates of these two species. A trophodynamic model is proposed to explain the observed abundance of prey in which nutrient concentrations and fish species abundance are the major driving forces.

Le régime alimentaire des gaspareaux (*Alosa pseudoharengus*) s'est modifié de façon appréciable au cours des années suivant la réduction des apports de phosphore dans le baie de Quinte. Une certaine variation du régime alimentaire a été notée chez les trois autres espèces étudiées, mais celle-ci n'était généralement pas significative. Les copépodes constituaient une plus grande partie de l'alimentation des gaspareaux, des éperlans arc-en-ciel (*Osmerus mordax*) et des bars-perches (*Morone americana*) après la réduction des apports de phosphore. Les poissons se nourrissant du macrozooplancton présentaient une préférence marquée pour les plus grosses espèces et évitaient les plus petites, tel que prévu par la théorie de la recherche de nourriture optimale. Le recoupement des régimes alimentaires du bar-perche et de la perchaude (*Perca flavescens*) n'était évident que dans la partie la plus en aval de la baie de Quinte. La compétition inter et intraspécifique pourrait expliquer les variations observées des taux de croissance chez ces deux espèces. L'auteur propose un modèle trophodynamique pour expliquer l'abondance des proies. Les principaux paramètres du modèle sont les concentrations de matières nutritives et l'abondance des espèces de poisson.

Introduction

The purpose of this paper is to document, qualitatively and quantitatively, the diets of four fish species that form a significant proportion of the fish biomass of the Bay of Quinte. These diets were examined in the periods before and after phosphorus control programs became fully effective. The fish species studied were the planktivorous alewife, *Alosa pseudoharengus*, and three other species: rainbow smelt, *Osmerus mordax*, white perch, *Morone americana*, and yellow perch, *Perca flavescens*. The latter three are best described as omnivorous over a wide size range, in that they eat zooplankton, benthos, and fish.

These data, in conjunction with estimates of prey abundance, were used to calculate the selectivity by predators for particular prey items. Optimal foraging theory predicts that animals forage so as to maximize fitness (Pyke et al. 1977). Therefore, the diet will be such that the net rate of energy intake is maximized (Pyke et al. 1977). Selection would be expected to be directed to larger prey which would, in turn, possibly result in a reduction in these preferred species.

Planktivores regulate both species composition and abundance of zooplankton (Hrbáček 1962; Brooks and Dodson 1965; Lynch 1979). The presence of large numbers of alewife in the bay may have been responsible for the observed abundance of small sized zooplankton and the paucity of large forms (Cooley et al. 1986). It is possible that the presence of alewife in the Bay of Quinte over the past 100 yr (Christie 1973) has restricted the size distribution of zooplankton. A reduction in larger zooplankton was reported in Lake Michigan in the mid-1960s when alewife became abundant (Wells 1970).

There is also evidence that community structure can modify the effects of nutrient inputs. Shapiro et al. (1975) and Lynch and Shapiro (1981) found that adding planktivorous fish to enclosures did not result in any change in phosphorus concentrations, but the mean total phytoplankton biomass increased 21 times above those enclosures that contained no fish. The trophic interactions ensuing from the abundance of planktivores in the 1970s and early 1980s (Hurley 1986a) may, therefore, be a major contributor to the high algal biomass of the Bay of Quinte.

These interactions are modelled for the Bay of Quinte to examine the possible effects that changing fish species composition, lowered concentration of both phosphorus and algae, and changes in zooplankton and macrobenthos populations might have on the aquatic community.

Methods

Fish Collection and Stomach Analysis

Six to 10 samples of alewife, rainbow smelt, white perch, and

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[1] Contribution 85-06, Ontario Ministry of Natural Resources, Fisheries Branch, Maple, Ont. L0J 1E0.

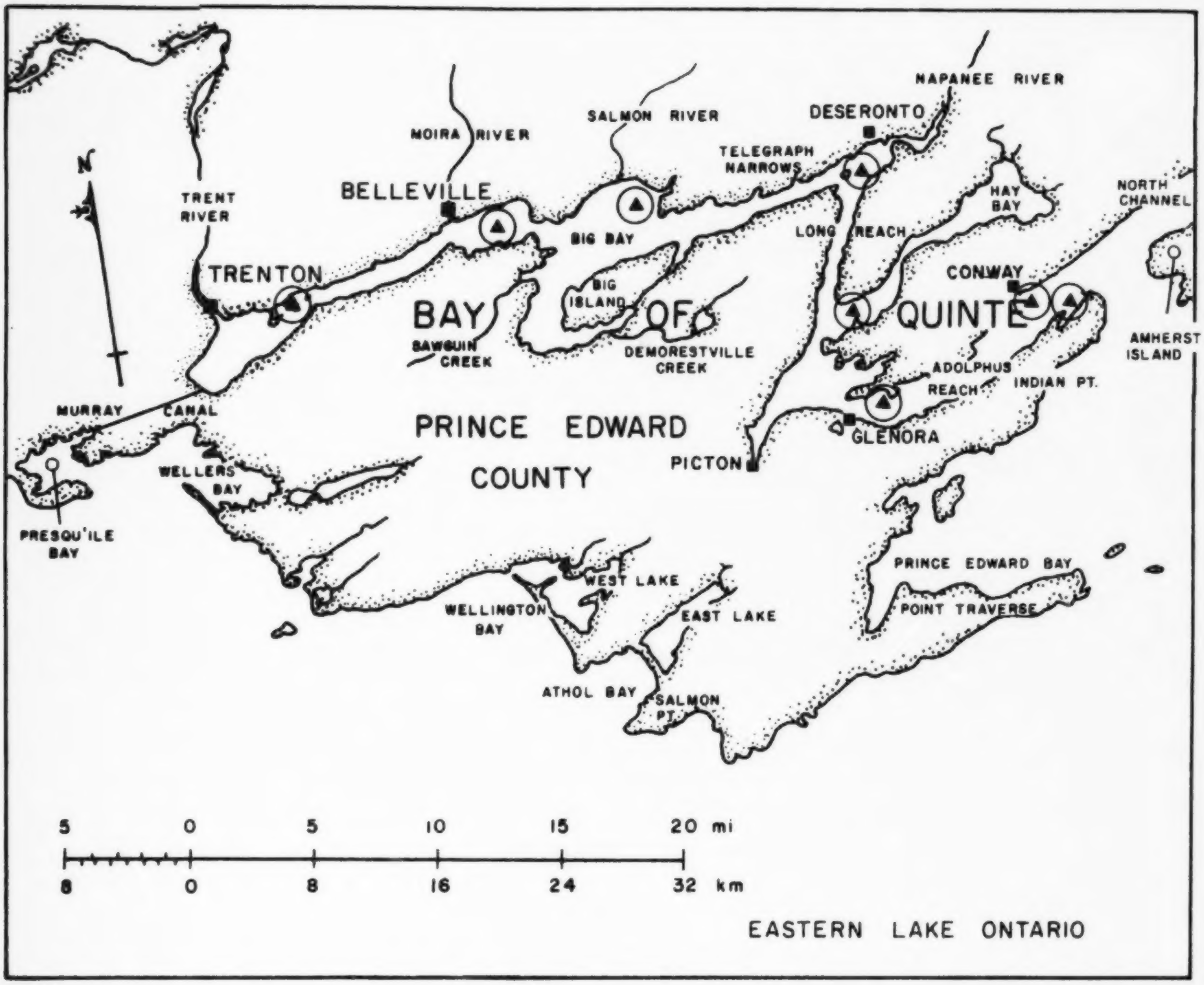
NAPANEE RIVER
SALMON RIVER
DESERONTO
MOIRA RIVER
TELEGRAPH NARROWS
N
TRENT RIVER
BELLEVILLE
NORTH CHANNEL
HAY BAY
BIG BAY
LONG REACH
TRENTON
BIG ISLAND
CONWAY
BAY OF QUINTE
AMHERST ISLAND
SAWGUIN CREEK
DEMORESTVILLE CREEK
ADOLPHUS REACH
INDIAN PT.
MURRAY CANAL
GLENORA
PRINCE EDWARD COUNTY
PICTON
WELLERS BAY
PRESQU'ILE BAY
PRINCE EDWARD BAY
WEST LAKE
WELLINGTON BAY
EAST LAKE
POINT TRAVERSE
ATHOL BAY
SALMON PT.
5 0 5 10 15 20 mi
8 0 8 16 24 32 km
EASTERN LAKE ONTARIO

FIG. 1. Locations of bottom trawling sites in the Bay of Quinte.

yellow perch were obtained from monthly bottom trawls made at up to eight locations between May and September each year from 1972 to 1981 (Fig. 1). Fork length and weight were recorded for each fish and stomachs were preserved in 10% buffered formalin.

Food items were identified, and estimates of biomass were calculated from measured lengths for chironomids, chaoborids, *Pontoporeia*, *Gammarus*, *Asellus*, and two species of sphaerids using equations from Johnson and Brinkhurst (1971). Weight values for macrozooplankton were obtained from N.H.F. Watson (unpublished data).

Estimation of Prey Abundance

Seasonal changes in the abundance of the major planktonic prey items were followed by weekly samples with a 30-L Schindler trap (Schindler 1969), fitted with a 75-μm-mesh bucket. Samples were taken at metre depth intervals at Belleville and Napanee and at greater intervals in the deeper stations at Glenora and Conway (Fig. 1). Samples were taken for 2 yr before phosphorus control (1975, 1976) and for 5 yr after phosphorus control (1979–83).

The macrobenthos was sampled with a 22.5 × 22.5 cm Eckman dredge (Johnson and McNeil 1986). The samples were screened through 0.6-mm-aperture brass screens. Index stations at Big Bay, Glenora, and Conway (Fig. 1) were sampled during August of 1972 and 1977, prior to complete phosphorus control, and in 1982 when phosphorus control had been present for 4 yr.

Measures of Diet Similarity

Changes in diets before and after phosphorus control were examined by two methods for measuring diet similarity or overlap. The null hypothesis states that there is no change in the diets.

The Schoener (1970) overlap index, a, is measured by

$$(1)\quad a = 1 - 0.5\left(\sum_{i=1}^{n} |Pxi - Pyi|\right)$$

where Pxi = proportion of food type i in the diet of fish species x, Pyi = proportion of food type i in the diet of fish species y, and n = number of food types.

The Spearman rank correlation coefficient, r_s (Steel and

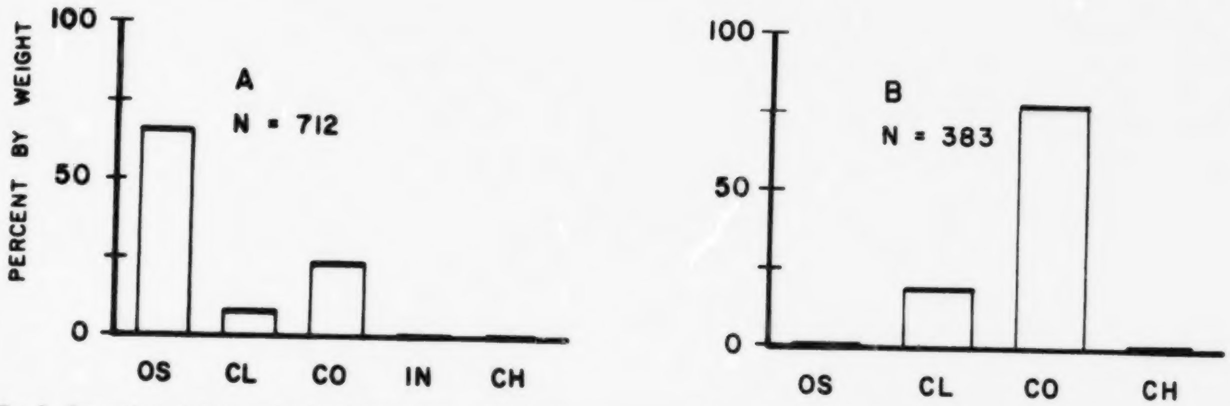

FIG. 2. Percent by weight of diet items of alewife before and after phosphorus control, Bay of Quinte. A, Before control, 1972–74; mean weight per stomach 16.42 mg ash-free dry weight. OS, ostracods; CL, cladoderans; CO, copepods; IN, insects; CH, chironomids. (A) (B) After control, 1978–80; mean weight per stomach 9.58 mg ash-free dry weight.

Torrie 1960), is measured by

$$(2)\quad r_s = 1 - \frac{6 \sum_{i=1}^{n} d_i^2}{(n-1)n(n+1)}$$

where d_i = difference between ranks of each food type and n = number of food types.

Significant overlap or diet similarity is considered to occur when the Schoener index exceeds 0.60 (Wallace 1981). The Spearman coefficient ranges between − 1 and + 1 and may be tested for significance by a t-test.

The percent of the total weight of particular diet items was used to measure overlap for each species of fish examined. Although it is recognized that the different methods of diet measure have advantages and disadvantages, the weight method should be representative of the caloric intake of the predator provided the items are of similar size (Wallace 1981). This criterion is generally met here, except in cases where fish were eaten. However, fish were not major diet items (as percent of total weight) for any species examined.

Calculation of Food Preference and Electivity

Chesson (1978, 1983) defined an estimator of food preference, α_i, which is the proportion of the diet which would consist of food type i if all food types were present in equal numbers in the environment. In this form, therefore, it can be used to detect changes in feeding behaviour through changes in the preference index (Chesson 1983). Symbolically, the relationship is

$$(3)\quad \alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j},\ i = 1, \ldots, m$$

where r_i is the number of items of food type i in the predator's diet, n_i is the number of food type i present in the environment, and m is the number of food items.

An extension of this index to examine electivity was suggested by Chesson (1983) since the value of α_i is equal to $1/m$ when selection is random, so that α_i will vary with the number of food types. To avoid this, he proposed that the preference for any type be relative to the average preference for all other food types. This was termed electivity, ε_i, and is calculated by

$$(4)\quad \varepsilon_i = \frac{m\alpha_i - 1}{(m-2)\,\alpha_i + 1},\ i = 1, \ldots, m$$

where m is 2 or greater. The advantage of this index over Ivlev's (1961) is that the new index is not subject to variations in food density.

Results

Stomach Contents Before and After Phosphorus Control

Alewife

Diets of alewife of all size ranges and in all locations in the bay were similar during the periods before and after phosphorus control. For this reason, all data were pooled to examine changes as a result of phosphorus control.

Before phosphorus control, ostracods were the main dietary item and accounted for about 70% of the mean weight of the stomach contents (Fig. 2). The proportion of ostracods increased as alewife size increased (0–60% in alewife 40–79 mm, 30–85% in alewife 80–199 mm). Copepods, primarily *Cyclops bicuspidatus thomasi*, were the next most common food item. Cladocerans, primarily *Eubosmina coregoni* and *Bosmina longirostris*, and to a much lesser extent, *Leptodora kindtii* and *Daphnia* spp., formed the next most important food items. Chironomids and insects were other minor diet items.

After phosphorus control, ostracods became a minor item while copepods, and to a much lesser extent, cladocerans became the most important components of the diet (Fig. 2). Copepods were 30–70% of the diet in the upper and middle bay and 80–95% of the diet in the lower bay. *Cyclops bicuspidatus thomasi* was the major copepod with *Mesocyclops edax* and *Cyclops vernalis* the next most common forms. Among the cladocerans, numbers of *Bosmina longirostris* and *Eubosmina coregoni* eaten fell substantially while numbers of *Chydorus sphaericus*, *Daphnia* sp., and *Leptodora kindtii* rose.

Both measures of diet similarity support the conclusion that alewife diets changed after phosphorus control (Table 1).

The mean weight of stomach contents decreased by 42% in the period after phosphorus control.

Rainbow smelt

Rainbow smelt were common only in the middle and lower bay, from Glenora to Indian Point (Fig. 1). In the period before

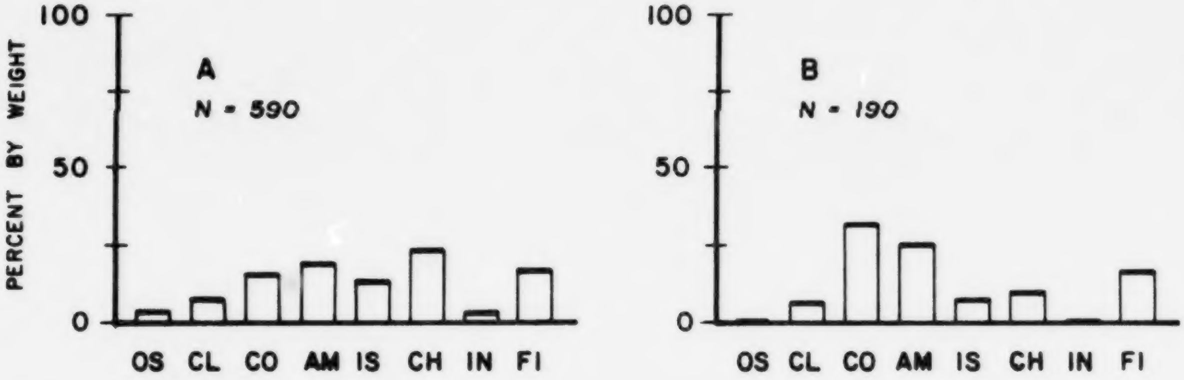

FIG. 3. Percent by weight of diet items of rainbow smelt before and after phosphorus control, Bay of Quinte. OS, ostracods; CL, cladocerans; CO, copepods; AM, amphipods; IS, isopods; CH, chironomids; IN, insects; FI, fish. (A) Before control, 1972–76; mean weight per stomach 1.30 mg ash-free dry weight. (B) After control, 1978; mean weight per stomach 2.38 mg ash-free dry weight.

TABLE 1. Calculated indices of diet similarity for fish species examined before and after phosphorus control.

Fish species	Schoener overlap index, a	Spearman rank correlation coefficient, r_s
Alewife	0.14	0.12[a]
Rainbow smelt	0.65	0.72[b]
White perch		
Upper-middle bay		
0–99 mm	0.63	0.86[c]
100–149 mm	0.78	0.42[a]
150–250 mm	0.91	0.72[c]
Lower bay		
0–99 mm	0.64	0.76[c]
100–149 mm	0.57	0.56[a]
150–250 mm	0.70	0.70[c]
Yellow perch		
Upper-middle bay	0.66	0.37[a]
Lower bay	0.79	0.89[c]

[a] Not significantly different from 0.
[b] $P < 0.001$.
[c] $P < 0.05$.

phosphorus control amphipods, isopods, copepods, chironomids, and fish were all of nearly equal weight in the diet with ostracods, cladocerans, and insects forming minor proportions (Fig. 3). Among smaller rainbow smelt, 60–79 mm, copepods formed from 45 to 70% of the diet.

After phosphorus control, copepods became even more prominent in the diet — up to 90% among the smaller fish — while amphipods and isopods became more important in diets of rainbow smelt over 120 mm. The proportion by weight of chironomids, insects, and fish remained almost the same in the two periods. The mean weight of stomach contents almost doubled in the period after phosphorus control.

The diet of rainbow smelt before and after phosphorus control showed significant overlap, and the Spearman rank correlation coefficient was highly significant (Table 1). This resulted from the fact that the proportions of major items such as amphipods, isopods, chironomids, and fish remained nearly the same before and after phosphorus control.

White perch

White perch diets varied significantly within the periods before and after phosphorus control with respect to both location (upper-middle, lower bay) and fish size.

In the upper-middle bay, chironomids formed the major biomass of food among all size classes of white perch in the period before control (Table 2). Copepods, primarily *Cyclops bicuspidatus thomasi*, were the next most important food item, especially for white perch less than 99 mm. Other food items were of minor importance with the exception of fish in the 150–250 mm white perch size class.

In the period following phosphorus control, chironomids became less prominent in white perch diets, especially in fish less than 150 mm (Table 2). Copepods increased in importance as did cladocerans. Other diet items changed slightly.

These changes in relative importance of diet items after phosphorus control did not result in significant changes in the overlap indices (Table 1), because the relative proportions of minor items changed little. The Spearman rank correlation coefficient was significant for all size classes but the 100–149 mm class (Table 1). This probably occurred because the coefficient is sensitive to changes in proportions of the less important items in the ranking procedure.

In the lower bay, amphipods, isopods, and chironomids were major food items for all sizes throughout the study (Table 3). Copepods, ostracods, and cladocerans were relatively minor diet items in the lower bay. The small sample (5) of white perch in the largest size class after phosphorus control makes any conclusions for this class tentative.

The mean weight of stomach contents increased dramatically among white perch in the upper-middle bay in the period after phosphorus control. Increases were observed in the smallest and largest size classes from the lower bay after phosphorus control.

Significant overlaps between diets in the periods before and after phosphorus control were evident for the 0–99 and 150–250 mm size classes, but not for the intermediate size class (Table 1). The high percentage of amphipods and low percentage of chironomids eaten in the period after control by the 100–149 mm class was sufficient to make the overlap nonsignificant.

Yellow perch

Stomach contents of yellow perch from the upper-middle bay (Trenton–Hay Bay) were significantly different from those from the lower bay (Glenora–Conway). In the upper-middle bay, chironomids were the major food item both before and after phosphorus control (Fig. 4). After control, fish were a larger proportion of the total weight of the diet, and cladocerans

TABLE 2. Percent composition by weight of stomach contents of white perch from the upper and middle Bay of Quinte in periods before and after phosphorus control (sample size in parentheses).

Food type	Fish size range, mm					
	0–99		100–149		150–250	
	Before control (54)	After control (149)	Before control (164)	After control (53)	Before control (420)	After control (216)
Ostracods	1.3	3.4	3.3	3.9	1.3	0.3
Cladocerans	3.8	9.3	0.7	4.9	0.2	2.4
Copepods	37.0	66.8	7.2	11.7	1.3	1.1
Amphipods	4.8	3.1	0.9	6.1	1.2	3.2
Isopods	1.0	<0.1	0.1	0.9	0.4	2.0
Molluscs	<0.1	0	4.0	0.8	1.3	0.5
Chironomids	50.7	17.0	81.9	63.1	68.7	61.6
Insects	0.8	0	0.5	2.5	0.3	0.8
Fish	0	0	0	5.4	25.1	27.8
Mean weight per stomach, mg ash-free dry weight	3.95	4.74	8.18	15.19	19.29	39.63

TABLE 3. Percent composition by weight of stomach contents of white perch from the lower Bay of Quinte in periods before and after phosphorus control (sample size in parentheses).

Food type	Fish size range, mm					
	0–99		100–149		150–250	
	Before control (83)	After control (27)	Before control (108)	After control (17)	Before control (111)	After control (5)
Ostracods	4.9	5.3	1.3	0.3	0.1	0
Cladocerans	0.2	1.5	<0.1	<0.1	<0.1	<0.1
Copepods	2.8	8.9	0.2	0.3	<0.1	<0.1
Amphipods	41.7	52.7	29.9	72.0	37.8	32.8
Isopods	16.6	10.5	17.8	18.9	24.9	8.7
Molluscs	<0.1	0	6.1	0	3.0	0
Chironomids	31.5	20.9	42.5	8.5	31.6	58.3
Insects	1.2	<0.1	2.0	0	2.5	0
Fish	0	0	0	0	0	0
Mean weight per stomach, mg ash-free dry weight	4.61	5.54	20.41	18.20	46.50	73.67

formed a small proportion of the diet by weight.

In the lower bay, amphipods, isopods, chironomids, and fish were fairly evenly represented in the total diet by weight before phosphorus control. After phosphorus control, chironomids were more prominant in the diet, with amphipods and isopods reduced somewhat (Fig. 4). Cladocerans and copepods were essentially absent from the diet in the lower bay.

Reductions in the mean weight of stomach contents were observed in the period after phosphorus control in both areas of the bay. These reductions amounted to 31% in the upper-middle bay and 15% in the lower bay.

According to the Schoener index, significant overlap of diet occurred both in the upper-middle and in the lower bay between the before and after phosphorus control period (Table 1). The Spearman rank correlation coefficient was, however, significant only in the lower bay. The lack of diet overlap in the upper-middle bay, according to the Spearman coefficient, was caused by the fact that cladocerans became important in diets in the after control period. Relatively minor diet items, isopods and insects, were less important in the after control period.

Stomach Contents in Relation to Prey Abundance

The frequency with which particular food items appear in the stomachs was compared to the numerical abundance of the same item in the water column. Some assumptions were made concerning the distribution of various prey species in order to facilitate comparisons. The mean seasonal (May–Oct.) abundance was used in spite of the fact that peaks and troughs occur at times during that period (Cooley et al. 1986). Abundance of some forms (e.g. harpacticoids) is probably underestimated by the Schindler trap since these species tend to stay near the bottom and in weedy areas (Ward and Whipple 1959). The abundance of bottom-dwelling ostracods, *Pontoporeia hoyi*, *Gammarus fasciatus*, *Asellus militaris*, chironomids, and chaoborids was estimated on a volume basis by dividing the areal abundance by the mean depth of water.

Alewife

The abundance of food items in 193 alewife stomachs from 1980 was compared to the numbers/m^3 obtained from plankton sampling (Table 4). Calculated values for α_i, the index of prey preference, and ε_i, the index of electivity, show that the most commonly found food items were not being actively selected from the plankton population. Those species that were being actively selected include the large calanoids, *Limnocalanus macrurus* and *Diaptomus sicilis*. The abundant, small

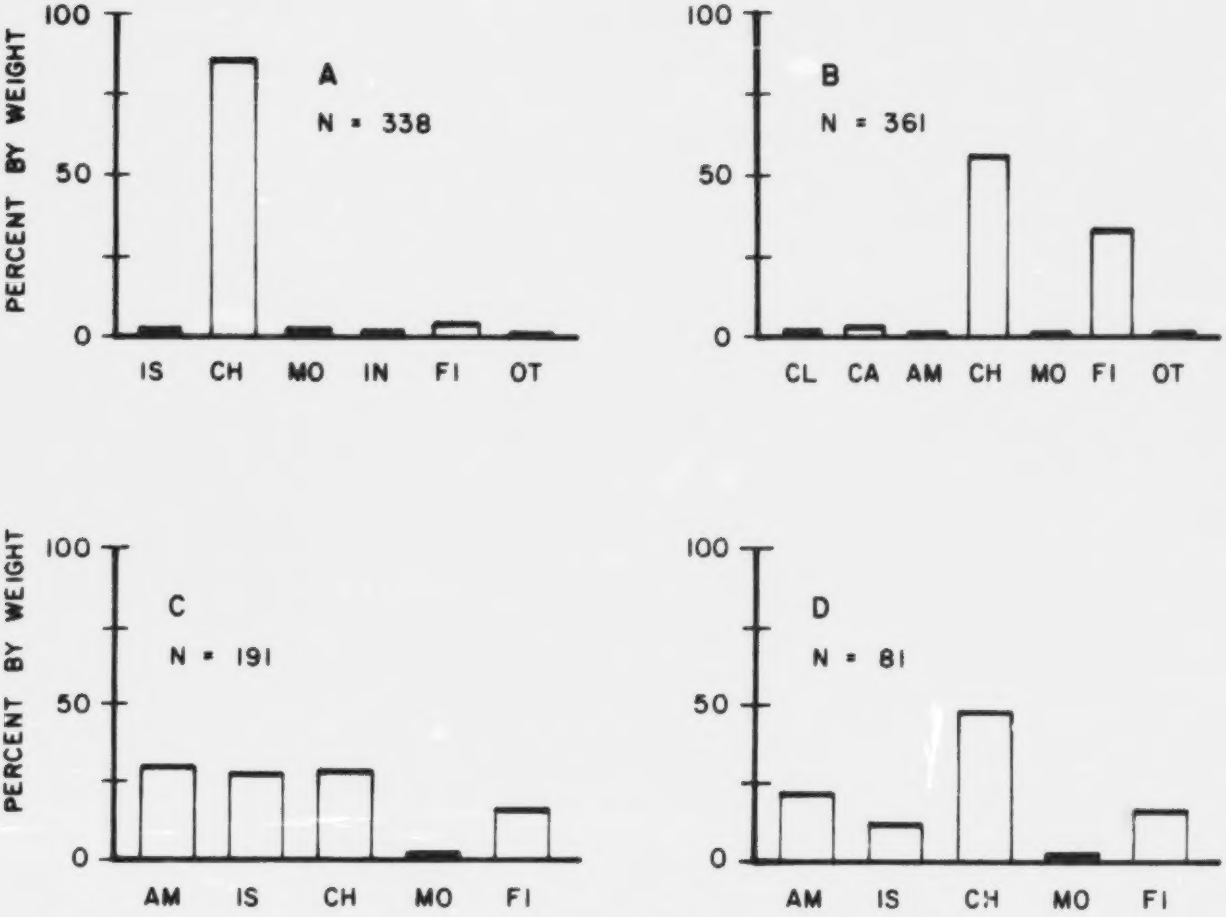

FIG. 4. Percent by weight of diet items of yellow perch from the upper-middle and lower Bay of Quinte before and after phosphorus control. CL, cladocerans; CA, chaoborids; AM, amphipods; IS, isopods; CH, chironomids; MO, molluscs; IN, insects; FI, fish; OT, other. (A) Before control, 1972–75; upper-middle bay, mean weight per stomach 12.37 mg ash-free dry weight. (B) After control, 1978, 1980, 1981; upper-middle bay, mean weight per stomach 8.55 mg ash-free dry weight. (C) Before control, 1972–75; lower bay, mean weight per stomach 25.36 mg ash-free dry weight. (D) After control, 1978, 1980, 1981; lower bay, mean weight per stomach 21.67 mg ash-free dry weight.

cladocerans were not being actively selected. The cyclopoid *Cyclops bicuspidatus thomasi* was a common item in the diet and, together with *Mesocyclops edax* and *Cyclops vernalis*, accounted for the major biomass in the alewife stomachs. It appears, however, that alewives avoided small plankton and attempted to capture larger ones during feeding.

White perch

White perch in the upper and middle bay actively selected large *Daphnia pulex* (14.8 μg), *Latona setifera* (5.0 μg), and *Ilyocryptus spinifer* (3.0 μg) over small abundant cladocerans, such as *Bosmina longirostris* and *Eubosmina coregoni* (Table 5). Cyclopoid copepods were eaten in large numbers, but not in proportion to their abundance. This resulted in large negative values for the electivity index. Harpacticoids were freqently eaten, and because of their habit of staying in the littoral zone, appear to be actively selected by white perch.

In the lower bay, white perch diets were radically different compared to the upper and middle bay (Table 6). Forms actively selected were chironomids, *Gammarus fasciatus*, *Asellus militaris*, *Latona setifera*, and *Alona affinis*. Except for the last two named species, plankton forms were avoided even though their mean number in the stomachs was sometimes large. *Pontoporeia hoyi* was the most numerous of the forms eaten by white perch and was neither selected nor avoided by them ($\epsilon_i \sim 0$). Again, the white perch were apparently avoiding the numerous cyclopoid copepods and cladocerans.

Yellow perch

Yellow perch from the upper and middle bay in 1980 and 1981 selected *Daphnia pulex* and *Eurycercus lamellatus* as preferred diet items, and did not select preferentially the more numerous small cladocerans, cyclopoid and calanoid copepods, and ostracods (Table 7).

In the lower bay, yellow perch selected chironomids, *Gammarus fasciatus*, and *Asellus militaris* (Table 8). They did not select *Pontoporeia hoyi*, ostracods, chaoborids, and planktonic cladocerans and cyclopoid copepods. This occurred in spite of the fact that *Pontoporeia hoyi* accounted for 13% by weight of the yellow perch diet.

Similarity of diets

White perch and yellow perch share many of the same food items (Table 5, 6, 7, 8) and can thus be considered as potential competitors. However, examination of the diets of these species in the post-phosphorus control period showed no significant

TABLE 4. Comparison of numbers of prey items per stomach in 193 alewife in 1980 from the Bay of Quinte, May–Sept., with mean seasonal abundance of prey from plankton samples in the same period. The mean dry weight of the prey item, an index (α_i) of prey preference, and an index of electivity (ε_i) are given.

	Number/ alewife stomach	Number/m^3	Mean weight, µg dry weight	α_i	ε_i
Cyclopoid copepodites	664.5	21740	2.8[a]	0.005	−0.809
Eubosmina coregoni	569.7	44872	1.9	0.002	−0.919
Chydorus sphaericus	312.6	21658	1.0	0.002	−0.919
Cyclops bicuspidatus thomasi	301.8	974	3.2	0.046	0.006
Bosmina longirostris	83.5	22517	1.8	0.001	−0.959
Mesocyclops edax	62.3	587	6.5	0.016	−0.491
Daphnia sp.	61.9	4664[b]	9.2[c]	0.002	−0.919
Daphnia retrocurva	61.8	11775	3.6	0.001	−0.959
Cyclops vernalis	37.0	788	3.5	0.007	−0.742
Daphnia galeata mendotae	23.5	2095	14.8	0.002	−0.919
Leptodora kindtii	14.0	159	14.8	0.013	−0.567
Calanoid copepodites	10.5	1049	5.6	0.001	−0.959
Copepod nauplii	5.8	15257	0.5[d]	0	−1
Limnocalanus macrurus	4.9	1	20.4[e]	0.727	0.965
Diaptomus oregonensis	4.6	39	9.3	0.017	−0.467
Diaphanosoma birgei	3.3	1117	4.0[f]	0	−1
Daphnia pulex	1.5	122	14.8[g]	0.002	−0.919
Diaptomus sicilis	1.5	2	12.3	0.111	0.448
Diaptomus siciloides	1.0	248	7.5	0.001	−0.959
Copepoda	0.9	100	5.0[h]	0.001	−0.959
Ceriodaphnia pulchella	0.9	7	1.8	0.019	−0.422
Eurycercus lamellatus	0.8	5	3.0	0.024	−0.319

[a] Mean of three species.
[b] Mean of all *Daphnia* spp. abundance used.
[c] Mean of all *Daphnia* spp.
[d] Mean of several spp.
[e] Value for stage 5, ranges from 1.8 µg at stage 1 to 8.2 µg at stage 4.
[f] Value for *Diaphanosoma leuchtenbergianum*.
[g] Value for *Daphnia galeata mendotae* used.
[h] Estimated from other copepods.

overlap in the upper-middle bay ($a = 0.43$, $r_s = 0.39$, $P > 0.05$). This was in spite of the fact that both species contained relatively large numbers of *Daphnia pulex* and *Eurycercus lamellatus*, which they strongly prefer (Table 5, 7). White perch and yellow perch did not share, to any significant degree, *Cyclops vernalis* and cyclopoid copepodites. White perch consumed considerably more of these species than did yellow perch. Other diet items that were commonly available such as chironomids, ostracods, *Bosmina longirostris*, *Eubosmina coregoni*, *Chydorus sphaericus*, and cyclopoid copepodites were not favoured diet items and were present in relatively few numbers in both species.

An examination of the diets of these two species in the lower bay (Table 6, 8), however, showed a significant overlap by Schoener's index, $a = 0.62$, but not by the Spearman rank correlation coefficient, $r_s = 0.28$, $P > 0.4$. Again, the difference between these indices is in the importance given by the Spearman index to differences in the food items of intermediate rank in the diet of one species but not of the other. *Pontoporeia hoyi* was the most numerous item in both species, while cyclopoid copepodites and *Mesocyclops edax* were numerous in white perch, but virtually absent in yellow perch stomachs. *Gammarus fasciatus* and *Asellus militaris* were numerous in yellow perch stomachs, but not in white perch stomachs.

The presence of *Mesocyclops edax* in white perch stomachs indicates that they were feeding pelagically, while the presence of shallow water forms such as *Gammarus fasciatus* in yellow perch stomachs indicates that they were feeding littorally. *Asellus militaris* tends to be more widely spread from the littoral to the sublittoral and profundal zone in the lower bay (M. G. Johnson, GLFRL, Owen Sound, Ont., pers. comm.). Yellow perch were preying upon *Asellus militaris* and both white perch and yellow perch were preying heavily upon *Pontoporeia hoyi*. This latter species is most abundant in the intermediate depth zones of the lower bay (Johnson and McNeil 1986). Overlap, and presumably competition, would therefore be most pronounced when white perch and yellow perch were feeding in the offshore, deeper zones of the lower bay.

Discussion

The effect of reduced phosphorus inputs on phosphorus levels in the bay has been discussed by Robinson (1986) and the effects on phytoplankton have been discussed by Nicholls et al. (1986). Zooplankton biomass changed relatively little as a result of phosphorus control measures with small cladocerans still dominant but some larger forms more abundant than before phosphorus control (Cooley et al. 1986). Macrobenthos biomass declined as phosphorus inputs were reduced, possibly because of a decline in productivity, while pollution-tolerant forms declined as water quality improved (Johnson and McNeil 1986). Numbers of alewife and white perch declined in the late 1970s and early 1980s while yellow perch increased (Hurley 1986a). Numbers of piscivores, primarily walleye, increased in this period and appear to play a pivotal role in regulating prey species abundance (Hurley 1986a, 1986b).

Some of these changes at lower trophic levels have had effects on diet composition of the fish species examined here, par-

TABLE 5. Comparison of numbers of prey per stomach in 206 white perch in 1980 and 1981 from the upper-middle section of the Bay of Quinte with estimated prey abundance. Calculated values for prey preference (α_i) and index of electivity (ε_i) are also given.

Food item	Number/ stomach	Number/ m^3	α_i	ε_i
Daphnia pulex	243.0	85	0.129	0.513
Cyclops vernalis	206.4	752	0.012	−0.594
Cyclopoid copepodites	128.4	24176	0	−1
Harpacticoida	41.9	10[a]	0.189	0.661
Alona affinis	31.0	48	0.029	−0.229
Ostracoda	24.8	14737	0	−1
Eurycercus lamellatus	19.6	6	0.147	0.567
Eubosmina coregoni	11.8	45776	0	−1
Leptodora kindtii	11.6	233	0.002	−0.919
Chironomidae	10.8	263	0.002	−0.919
Chydorus sphaericus	9.2	25215	0	−1
Mesocyclops edax	6.6	583	0.001	−0.959
Ilyocryptus spinifer	6.0	1	0.270	0.772
Daphnia galeata mendotae	3.8	4588	0	−1
Latona setifera	3.8	1	0.171	0.625
Daphnia retrocurva	3.7	15049	0	−1
Chaoborinae	3.1	263	0.001	−0.959
Eurytemora affinis	2.5	52	0.002	−0.919
Cyclops bicuspidatus thomasi	2.2	283	0	−1
Diaphanosoma birgei	1.4	1221	0	−1
Bosmina longirostris	1.4	45199	0	−1
Macrocyclops albidus	1.0	1	0.045	−0.005

[a] Abundance estimate increased by 10× to account for undersampling.

TABLE 6. Comparison of number of prey per stomach in 35 white perch in 1980 and 1981 from the lower Bay of Quinte with estimated prey abundance. Calculated values for prey preference (α_i) and index of electivity (ε_i) are also given.

Food item	Number/ stomach	Number/ m^3	α_i	ε_i
Pontoporeia hoyi	76.9	325	0.062	−0.039
Cyclopoid copepodites	30.1	25035	0	−1
Mesocyclops edax	18.9	430	0.011	−0.731
Ostracoda	18.8	2368	0.002	−0.945
Chironomidae	7.5	21	0.093	0.179
Cyclops vernalis	5.5	172	0.008	−0.797
Gammarus fasciatus	3.2	7	0.119	0.308
Leptodora kindtii	2.5	43	0.015	−0.649
Asellus militaris	2.5	4	0.163	0.463
Eubosmina coregoni	1.9	11226	0	−1
Cyclops bicuspidatus thomasi	1.3	2871	0	−1
Latona setifera	1.3	1	0.339	0.756
Eurytemora affinis	0.8	65	0.003	−0.919
Alona affinis	0.7	1	0.183	0.516
Daphnia retrocurva	0.4	4750	0	−1

ticularly alewife, and to a lesser degree, the other three species. However, alewives are sufficiently abundant to favour the production of smaller forms such as *Bosmina longirostris*. A similar finding was reported by Lynch (1979) where vertebrate planktivores in enclosures cropped larger plankton and smaller plankton proliferated.

Alewife diet showed a significant change between the periods before and after phosphorus control. The change was due almost entirely to the virtual elimination of ostracods from the diet and increased consumption of copepods after phosphorus control. *Cyclops bicuspidatus thomasi* was a major item in the diet after phosphorus control. *Limnocalanus macrurus* and *Diaptomus sicilis* were being positively selected, possibly because of their larger size.

If alewife choose diet items that would provide greatest caloric value, then selection of larger zooplankton would be expected. Similarly, items of low caloric value would be rejected, as they appear to be. These observations would be predicted by current optimal foraging theory (Lacher et al. 1982).

In alewife stomachs, items of small size are still the most numerous (Table 4) even though they are not being selected. This is presumably a consequence of the numerical abundance of these forms. Janssen (1978) has shown that alewife filter feed when microcrustacean abundance exceeds 100 000/m^3. Mean seasonal abundance in the Bay of Quinte averaged about 150 000/m^3, so that the presence in alewife stomachs of large numbers of presumably nonselected food items would be expected from this feeding behaviour.

Rainbow smelt showed relatively little change in their diet as a consequence of nutrient reduction. The increased consumption of cyclopoid copepods after phosphorus control was probably the result of the increased abundance of these forms in the lower bay where the majority of the rainbow smelt were taken.

White perch and yellow perch did not show a consistent, significant overlap in their diet. Growth rates of white perch fell markedly when their numbers were high, and then rose after 1978 when the population crashed (Hurley 1986a; Minns and Hurley 1986). This indicated that intraspecific competition was relatively strong among white perch. The fact that food consumption increased in the years after the population crashed argues that food limitation might have been responsible for the stunting observed in white perch.

Growth rates of yellow perch up to age 4 were not significantly affected by the changing biomass of white perch. They remained essentially constant from 1958, prior to the white perch dominance, through 1974 when white perch were most abundant. However, the mean lengths of yellow perch aged 5 yr and older were between 10 and 25 mm shorter in the years when white perch were most abundant. Yellow perch growth increased substantially in the years after the crash of the white perch. This would argue that increased food resources, made available when white perch declined, caused the increase in yellow perch growth. The data, however, show that the mean weight of stomach contents actually decreased in yellow perch after the decline in white perch abundance. Yellow perch in the upper-middle bay consumed more fish in the period after phosphorus control.

The growth rate of yellow perch increased after the decline in white perch occurred even though yellow perch abundance was increasing (Hurley 1986a). This would indicate that intraspecific competition in yellow perch may not be as strong as interspecific competition with white perch.

The trophic dynamic model which these observations would support can be outlined as follows. Nutrient reduction in the late 1970s decreased algal production and increased the food chain functional forms, which favoured the larger zooplankton species. These larger zooplankters, although favoured by the fish species studied here, were under reduced predation pressure. This occurred because of the lower alewife abundance from 1977 through 1983 in the upper-middle bay. This reduction was probably brought about by their increased predation by the expanding walleye population. White perch abundance also

Table 7. Comparison between food items in stomachs of 226 yellow perch fom the upper and middle Bay of Quinte, 1980 and 1981, and the abundance of same items in plankton nets and Eckman dredge hauls with calculated values for α_i, an estimator of preference, and ε_i, an index of electivity.

Food item	Number/ yellow perch stomach	Number/ m^3	α_i	ε_i
Daphnia pulex	74.0	85	0.315	0.747
Eurycercus lamellatus	8.8	6	0.531	0.889
Chironomidae	6.7	263[a]	0.009	−0.760
Chaoborinae	6.5	263[b]	0.009	−0.760
Eurytemora affinis	2.2	52	0.015	−0.628
Cyclops vernalis	2.2	752	0.001	−0.970
Cyclopoid copepodites	1.9	24176	0	−1
Ostracoda	0.68	14737[c]	0	−1
Eubosmina coregoni	0.64	45776	0	−1
Daphnia retrocurva	0.62	15049	0	−1
Mesocyclops edax	0.27	583	0	−1
Latona setifera	0.20	1	0.072	0.076
Daphnia galeata mendotae	0.17	4588	0	−1
Chydorus sphaericus	0.13	25215	0	−1
Ilyocryptus spinifer	0.13	1	0.047	−0.150
Calanoid copepodites	0.09	1669	0	−1

[a] Estimated by dividing areal abundance by mean depth.

[b] Abundance assumed similar to Chironomidae.

[c] Abundance data available for lower bay only, areal abundance divided by mean depth.

Table 8. Comparison between food items in stomachs of 67 yellow perch fom the lower Bay of Quinte, 1980 and 1981, and the abundance of same items in plankton nets and Eckman dredge hauls with calculated values for α_i, an estimator of preference, and ε_i, an index of electivity.

Food item	Number/ yellow perch stomach	Number/ m^3	α_i	ε_i
Pontoporeia hoyi	35.2	325	0.054	−0.321
Chironomidae	9.0	21	0.215	0.423
Gammarus fasciatus	5.9	7	0.423	0.737
Ostracoda	3.8	2368	0.001	−0.982
Asellus militaris	2.1	4	0.263	0.525
Chaoborinae	0.9	21	0.022	−0.663
Eurcercus lamellatus	0.09	2	0.023	−0.650
Eurytemora affinis	0.04	65	0	−1
Eubosmina coregoni	0.03	11226	0	−1
Cyclopoid copepodites	0.03	25035	0	−1

declined dramatically after 1978 because of a climate-related mortality. Their numbers remained low, probably due to walleye predation. Yellow perch numbers increased in this same period, but not to the extent that the white perch had fallen. Rainbow smelt were abundant only in the lower bay and would impact on chironomids, ostracods, amphipods, and in the years after phosphorus control, on cyclopoid copepods. The predation on larger zooplankters had decreased because of lower fish populations. However, the numbers of carnivorous species such as *Leptodora kindtii* and large cyclopoid and calanoid copepods were insufficient to exert appreciable pressure on the abundant, small herbivores, such as *Bosmina longirostris* and *Eubosmina coregoni*.

Benthic macroinvertebrates responded to reductions in phosphorus concentrations in the upper bay by increasing numbers of those species of chironomids and oligochaetes that are less tolerant of eutrophic conditions (Johnson and McNeil 1986). In the lower bay the abundance of *Pontoporeia hoyi* increased after 1977, probably because of reduced predation that occurred with the collapse of white perch. The increase in yellow perch in the lower bay increased the predation on *Gammarus fasciatus*, in particular, and resulted in a drop in the abundance of this species (Johnson and McNeil 1986).

Apparently, phosphorus control has had little impact on the diets of rainbow smelt, white perch, and yellow perch, but has had an affect on alewife. Any change occurred because of alterations in prey species composition, initiated by changes in algae composition and biomass. Although the selection for larger forms of zooplankton was strong, the decline in fish species that ate them was sufficient to prevent the elimination of these zooplankters. However, the numbers of these large, and primarily carnivorous forms were not great enough to impact on the herbivorous zooplankton.

The changes in the biota initiated by the reduction in phosphorus inputs have not permeated to all trophic levels in the bay in the early 1980s. Until these effects have been funneled through the longest lived organisms in the community, the species composition of the bay's ecosystem, and the numerical strength of species will not be fully established.

References

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. Science 150: 28–35.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59: 211–215.

1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64: 1297–1304.

Christie, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23: 65 p.

Cooley J. M., J. E. Moore, and W. T. Geiling. 1986. Population dynamics, biomass, and production of the macrozooplankton in the Bay of Quinte during changes in phosphorus loadings, p. 215–233. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Hrbaček, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Rozpr. Cesk. Akad. Ved. 72: 1–116.

Hurley D. A. 1986a. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. Growth, diet, and food consumption of walleye (*Stizostedion vitreum vitreum*): an application of bioenergetics modelling to the Bay of Quinte, Lake Ontario, population. p. 224–236. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, CN.

Janssen, J. 1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes *Coregonus hoyi* and *C. artedii*. J. Fish. Res. Board Can. 35: 249–253.

Johnson, M. G., and R. O. Brinkhurst. 1971. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1699–1714.

Johnson, M. G., and O. C. McNeil. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–84, p. 177–189. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Lacher, T. E. Jr., M. R. Willig, and M. A. Mares. 1982. Food preference as a function of resource abundance with multiple prey types: an experimental analysis of optimal foraging theory. Am. Nat. 120: 297–316.

Lynch, M. 1979. Predation, competition, and zooplankton community structure: an experimental study. Limnol. Oceanogr. 24: 253–272.

Lynch, M., and J. Shapiro. 1981. Predation, enrichment, and phytoplankton community structure. Limnol. Oceanogr. 26: 86–102.

Minns, C. K., and D. A. Hurley. 1986. Population dynamics and production of white perch, *Morone americana*, in the Bay of Quinte, Lake Ontario, population, p. 215–223. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, , p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137–154.

Robinson, G. W. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reduction in phosphorus loadings, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Schindler, D. W. 1969. Two useful devices for vertical plankton and water sampling. J. Fish. Res. Board Can. 26: 1948–1955.

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy environments. Ecology 51: 408–418.

Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: An ecosystem approach to lake restoration. *In* P.L. Brezonik and J.L. Fox (ed.), Water quality management through biological control. Report No. ENV-07-75-1, Univ. of Florida, Gainesville, FL.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York, NY.

Wallace, R. K. Jr. 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110: 72–76.

Ward, H. B., and G. C. Whipple. 1959. Fresh-water biology, 2nd edition, ed. W. T. Edmondson. John Wiley and Sons, Inc., New York, London, Sydney.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556–565.

Phosphorus Loadings and Environmental Quality in the Bay of Quinte, Lake Ontario

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Johnson, M. G. 1986. Phosphorus loadings and environmental quality in the Bay of Quinte, Lake Ontario, p. 247–258. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

This synthesis of Project Quinte data examines effects of magnitude and source of phosphorus (P) loadings, hydrology of the bay, and other factors on abundance and production of primary producers. Correlation and multiple regression analyses and two general deterministic models were used to interpret trends among years. Average seasonal algal biomass, chlorophyll *a* (Chl *a*) concentration, integral, and maximum volumetric rate (A_{max}) of primary production through 1972–82 were significantly correlated with point-source P loadings and percent point-source P but not with total P loading. Point-source P inputs were reduced from about 25 to 10% of total P loadings, and phytoplankton declined by 25–60% through the period. In multiple regression, P loading and flushing rate affected phytoplankton abundance and production more than water depth, radiation, and water temperature. Results from the Dillon–Rigler model, expanded to predict Chl *a*, transparency, macrophyte abundance, and P retention, were in good agreement with observations from 1972 to 1981. Main conclusions from application of the model to data from 1916 to 1981 were that accelerating point-source P loadings in 1956–66, aggravated by low river flows in 1962–66, led to 2 times the Chl *a* concentrations and a decline in macrophytes to one half of their former abundance, compared with 1916–55. During this early period, effects of total P loadings, often as high as in recent years, were offset by coincident changes in flushing rate, which contributed to stability in the primary producer system. During 1980 and 1981, P and Chl *a* concentrations declined to levels similar to those predicted in the 1930–55 period. Critical P loadings, calculated using Vollenweider's model, were close to actual river loadings during 1965–81, indicating that the bay lacked tolerance to increasing point-source P inputs. Phytoplankton abundance and production were correlated with the ratio of actual total P loading to critical P loading but not to total P loading.

La présente synthèse des données du projet de la baie de Quinte traite des effets du volume et de l'origine des charges de phosphore (P), de l'hydrologie de la baie et d'autres facteurs sur l'abondance et la production des producteurs primaires. Les tendances interannuelles ont été étudiées par analyses de corrélation et de régressions multiples et par l'application de deux modèles déterministes. De 1972 à 1982, les valeurs moyennes saisonnières de la biomasse des algues, de la concentration de la chlorophylle *a* (Chl *a*) et du taux volumétrique intégré et maximal (A_{max}) de la production primaire présentaient une corrélation significative avec les charges ponctuelles de P et le pourcentage des sources ponctuelles de P, mais non avec les charges de P totales. Pendant cette période, le pourcentage des rejets ponctuels de P, par rapport aux rejets totaux, est passé d'environ 25 % à 10 % et la quantité de phytoplancton a été réduite de 25 à 60 %. Les régressions multiples indiquaient que la charge de P et le taux de renouvellement des eaux avaient un effet plus important sur l'abondance et la production du phytoplancton que la profondeur de l'eau, le rayonnement et la température de l'eau. Les résultats du modèle de Dillon–Rigler, élargi à la prévision des valeurs de la Chl *a*, de la transparence, de l'abondance des macrophytes et de la rétention de P, correspondaient bien aux observations faites entre 1972 et 1981. L'application du modèle aux données de 1916 à 1981 a permis de conclure que l'augmentation des charges ponctuelles de P de 1956 à 1966, aggravée par les faibles débits de la période 1962–66, avait fait doubler les concentrations de Chl *a* et baisser de moitié l'abondance des macrophytes comparativement à la période 1916–55. Au cours de cette période, les charges de P total, souvent aussi élevées que celles des dernières années, étaient annulées par des modifications concurrentes du taux de renouvellement, ce qui a contribué à la stabilité du système de production primaire. En 1980 et 1981 les concentrations de P et de Chl *a* sont revenues à des valeurs semblables à celles prévues pour la période 1930–55. Les valeurs des charges critiques de P, calculées à l'aide du modèle de Vollenweider, s'approchaient des valeurs réelles des charges du cours d'eau pendant la période 1965–81, ce qui indique que la baie ne pouvait plus compenser les augmentations des rejets ponctuels de P. L'abondance et la production du phytoplancton étaient corrélées au rapport de la charge réelle de P total à la charge critique de P, mais non à la charge de P total.

Introduction

Phosphorus loading reduction is the primary element of a Canada–United States strategy to reduce the rate of eutrophication of the lower Great Lakes. The response of the Bay of Quinte, Lake Ontario, to reduced P inputs was studied by federal, provincial, and university scientists collaborating in Project Quinte (Johnson and Hurley 1986). P was reduced in detergents beginning in 1971 and P was removed at Quinte waste treatment plants by late 1977 to a residual 0.5 mg · L $^{-1}$ from May through September and to 1.0 mg · L $^{-1}$ in other months.

The Project Quinte group's specific objectives have been to evaluate the P-control program in terms of (1) P loadings and

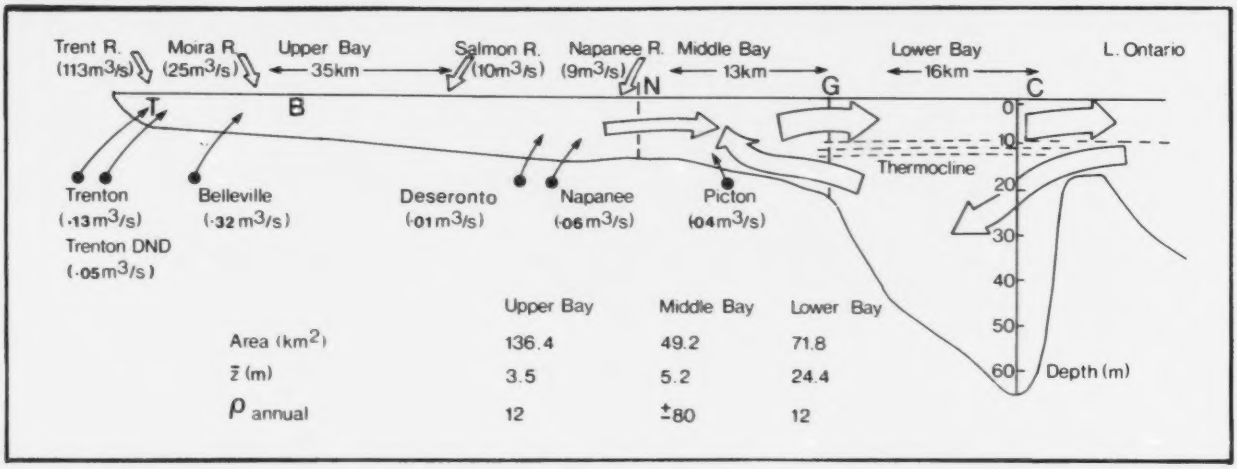

FIG. 1. Schematic diagram of the Bay of Quinte showing, from top to bottom, main rivers entering the bay and their mean annual flows, lengths of sections of the bay (upper, middle, and lower), limnological stations (T, Trenton; B, Belleville; N, Napanee; G, Glenora; C, Conway), waste treatment plants and their annual discharges to the bay, and data on area, mean depth, and flushing rate of the three main sections of the bay.

sources, ambient P concentrations, and environmental quality, (2) the significance of high flushing and turbulence in the upper bay and influx of lake water through the lower bay, (3) algae–macrophyte interactions, the role of macrophyte beds as a nutrient-sediment sink, and significance of changes in abundance of macrophytes, (4) relative significance of P loadings in relation to natural hydrologic and climatic factors, and (5) prospects for future enhanced environmental quality. Environmental quality improvement in the Bay of Quinte is assumed to mean reduction in frequency, duration and amplitude of algal blooms, increased diversity and moderate abundance of macrophytes, and better habitat for fish communities (for example, improved oxygen conditions, greater abundance of food-chain functional phytoplankton, and optimum macrophyte stocks).

The first nutrient budget for the Bay of Quinte, calculated for 1968 by Johnson and Owen (1971), showed that only 40% of P loading was from waste treatment plants and 60% was from nonpoint sources. However, river inputs were estimated to have much less impact than their major contribution to the absolute load would indicate, first, because much of the river inputs was flushed from the bay in the spring freshet, and second, because river P concentrations were generally lower than bay P concentrations. Johnson and Owen (1971) suggested that the high flushing rate of the bay would promote rapid improvement in environmental quality following point-source P reduction, but the extensive, shallow, P-enriched sediments in the upper bay might delay recovery.

Recent work has been concentrated on strengthening the data base of P inputs and environmental quality in the bay over time. Since 1972, monitoring of rivers and waste treatment plants provided a continuous data base on P loadings and also allowed filling in gaps from 1965 to 1967 and 1969 to 1971 (Minns and Johnson 1979). Minns (1986a) calculated earlier river loadings back to 1916 when flow measurement commenced and point-source inputs back to 1800 using population and detergent-use information. These, together with the data base on limnological characteristics of the bay examined weekly from May to October since 1972, now provide project participants with the opportunity to evaluate the P-removal program from a management perspective. This requires a better understanding of how factors such as flushing rate, lake water intrusions, bay depth, and seasonal climatic factors interact with changing point-source and river P loadings to affect availability and use of P by the aquatic community and resultant environmental quality.

This paper describes the changing magnitude and sources of P loadings and responses by primary producers on a year-to-year basis primarily by means of correlation analysis and relatively simple P-loading response models which have been useful for management purposes (Dillon and Rigler 1974; Vollenweider 1976). In the absence of historical data, these models provide a baseline description of the bay and suggest the important factors responsible for deterioration in environmental quality, which provide guidance, therefore, for remedial management. Findings on intraseasonal relationships of phytoplankton, macrophytes, and growth factors are reported elsewhere (Millard 1986; Nicholls et al. 1986; Crowder and Bristow 1986). Secondary production also is the subject of additional papers (Cooley et al. 1986; Johnson and McNeil 1986; Hurley 1986; and other papers in this volume).

The Bay of Quinte System

The chief features of the Quinte system include four main rivers which enter a shallow mixed upper bay, which leads to a deep lower bay and then to Lake Ontario (Fig. 1). The large watershed, about 18 000 km² and 70 times the area of the bay, contributes to a high and variable flushing rate and large P loadings in rivers. Waste treatment plants contribute declining P inputs mainly to the upper bay, with the three plants at Trenton and Belleville comprising over 80% of point-source inputs. The smaller middle bay is a zone of periodic mixing of upper bay water and entrained hypolimnetic water from the lower bay. Deeper waters of the lower bay stratify thermally in the summer, with advection of Lake Ontario water to the hypolimnion of approximately equal volume to that displaced from the middle bay. No major rivers or point-sources contribute additional nutrients to the lower bay. P inputs to the lower bay in both Lake Ontario and upper bay water have declined since commencement of the P-removal program. Additional background information on the Bay of Quinte and the P-removal program are provided by Johnson and Hurley (1986) and Sly (1986).

P Loadings and Environmental Quality

Trends in P Loadings

Monitoring of rivers and point sources since 1972 and model predictions of these inputs since 1916 provided a 66-yr series of P loadings to the Bay of Quinte. In 30 yr between 1916 and 1945, point-source inputs doubled; they doubled again in 15 yr between 1946 and 1960 and increased by one third in the next decade. Use of polyphosphate detergents commenced in the mid-1930's, and their contribution exceeded other sources of P in treatment plant wastes by 1962. Following legislated reductions in detergent P and some upgrading of waste treatment facilities, point-source P contributions declined to 67% during the period 1972–77. In the years since P removal at treatment plants, from 1978 on, point-source inputs declined sharply to 28% of point-source inputs in the peak years 1965 and 1968. Point-source P loadings decreased from a maximum of 40% of total annual loadings (1968) and an average of 25% (at average flushing rate) before P removal to about 10% of total loadings after P removal.

Total annual P loadings (sum of point-source and river loadings) were highly variable over the 1916–81 period and they were loosely correlated with river discharge and bay flushing rates. For example, river discharge in the upper bay from 1916 to 1981 accounted for only 42% of variability in P loading in the period May–October. However, periods of below average P loading coincided with low river discharges and flushing rates in earlier years. The seven years 1930–36 had below average loadings and river discharges, as did 8 of 10 years in the 1916–25 period. A trend in increasing P loadings attributable to accelerating point-source P inputs was evident by 1962. From 1962 to 1977, 13 of 16 years had *above average* P loadings and *below average* river discharges and flushing rates.

Appropriate time frames for comparison of P loadings with measurements of environmental quality are the May–October period for the upper bay and annual for the lower bay. Because of large temporal and spatial variations in hydrological characteristics of the bay and rivers, annual P loadings to the whole bay have minimal value in interpretation of limnological and environmental quality responses of the bay taken as a single unit. Although the upper bay received almost all of the bay inputs of water and nutrients from rivers and point sources, the annual flushing rate of the upper bay is so large, 9.2–14.6, that winter and early spring P inputs probably have a minor influence on summer conditions. Flushing rates during May–September varied from about 1 to 4.6 in the 1965–81 period. Only about one quarter of the annual flow entered the bay during that 5-mo period. Therefore, in a later section, the "summer" loadings are used in modelling the response of the upper bay. Annual loadings appear to be satisfactory for interpretation of lower bay limnology, with annual flushing rates of about 3–4.6. However, there is an additional hydraulic and nutrient loading by the deepwater intrusion of Lake Ontario water which mixes in the middle bay with the outward flow from the upper bay. This loading will be incorporated in a model of the lower bay response.

Trends in P Concentrations

P concentrations declined, especially in the upper bay, apparently in response to point-source P reductions. In comparing the 1972–77 and 1978–81 periods, P concentrations declined by 28, 38, and 34% at the Trenton, Belleville, and Napanee stations, respectively. The decline was less at Hay Bay, by 22%, and at Glenora, by 15%. No change was apparent at the Conway station. Point-source P loading declined from 25 to 10% of the total loading from 1972–77 to 1978–81. Therefore, the decline in P concentration at upper bay stations reflected the decline in point-source inputs more than middle and lower bay stations, indicating a diminishing response toward the mouth of the bay. The lower bay nutrient regime appeared to be uncoupled from that of the upper bay, thus emphasizing the apparent importance of intrusions of lake water into the lower bay.

Trends in Abundance and Production of Phytoplankton

Average algal biomass (May–September) declined from the pre-P control period to post-P control period by about 50% at Belleville and Napanee stations and less at Hay Bay and Glenora, by about 40 and 25%, respectively (Nicholls et al. 1986). Surprisingly, algal biomass declined by 40% at Conway although no change in P concentrations was detected. Chlorophyll *a* (Chl *a*) concentration showed a more uniform diminishing trend toward the bay mouth, with 50% decline in phytoplankton density at Belleville and Napanee, 25% decline at Glenora, and 20% decline at Conway. At the Belleville and Napanee stations, seasonal mean primary production declined by 46 and 37%, respectively, between periods. In the middle and lower bay, primary production decreased by approximately 25%. Reductions in maximum volumetric rate (A_{max}) of primary production between periods were similar (Millard and Johnson 1986).

Correlation analysis was used to test relationships between P loading (point source, total, and percent point source) and phytoplankton abundance and production at the Belleville and Conway stations. There was a strong relationship between point-source P loadings and each of the four phytoplankton variables at the Belleville station (Fig. 2). Pre-P control and post-P control clusters are obvious in each plot. Point-source P loadings accounted for the following percentages of variability (r^2) in each variable: 80% in integral primary production and A_{max}, 47% in Chl *a* and 79% in algal biomass. Point-source P input, as a percentage of total P loading, also was closely correlated with the four variables, accounting for 60% of the variability in integral primary production and A_{max}, 51% in Chl *a* and 71% in algal biomass. Total P loadings did not correlate with any of the four variables at the Belleville station (Fig. 2).

Correlations between P loadings and responses of phytoplankton were considerably weaker at the Conway station (Fig. 2). No significant correlations between total P loading and the four variables were observed. Only one variable, algal biomass, showed significant correlation ($r^2 = 40\%$) with percentage point-source P. All variables were correlated with point-source P loading. Three variables were strongly correlated ($r^2 > 60\%$), but only 37% of the variability in Chl *a* was accounted for by point-source P loading.

Multiple regression analysis was used to assess the relationship of algal abundance and production to external factors. Each of three dependent variables, Chl *a*, algal biomass, and integral primary production, using May–October means for the years 1972–81, was related to five variables determined independently of water chemistry variables such as P concentration. These five variables were flushing rate, total P loading in the May–October period, mean bay depth, incident radiation, and surface water temperature, used in stepwise regression in that order. This analysis was carried out with Belleville data, using upper bay P loadings, and with Conway data, using whole-bay P loadings. Seasonal mean radiation and temperature were least

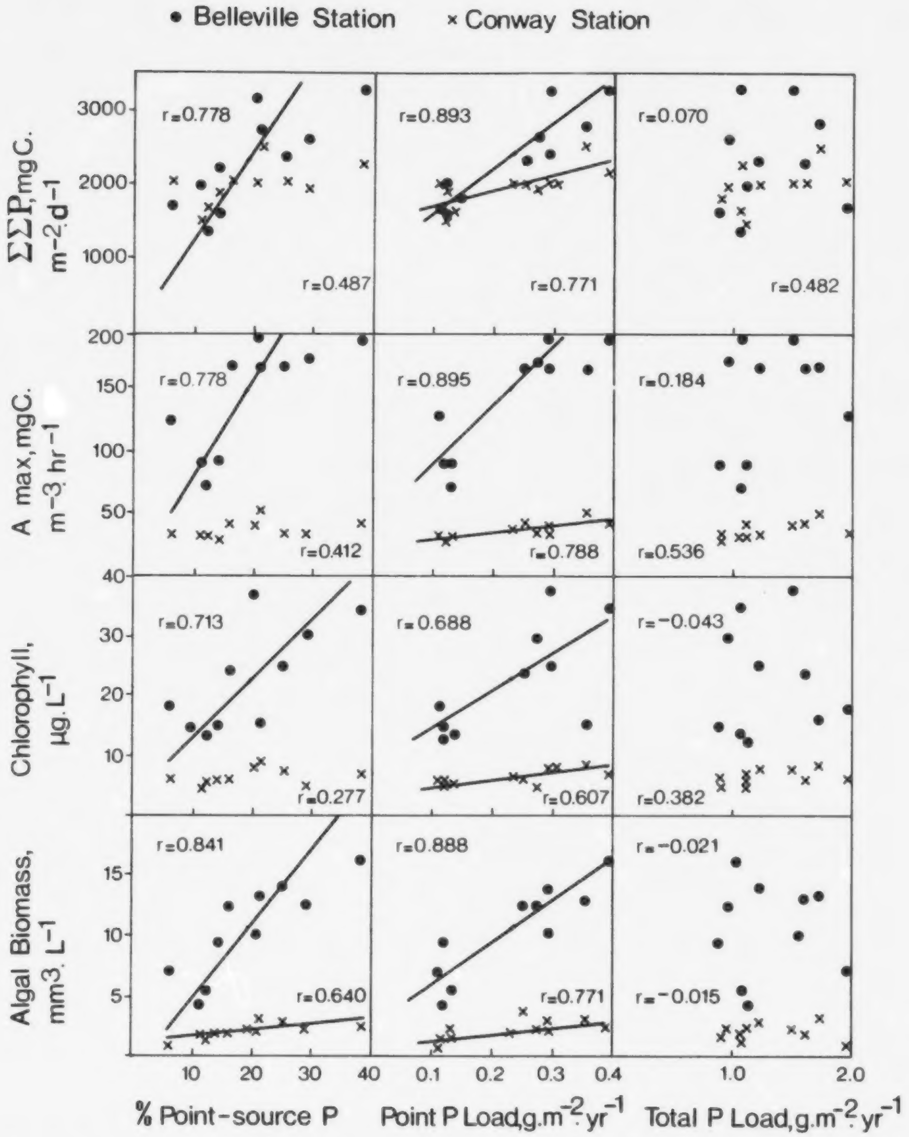

FIG. 2. Correlation analyses of seasonal means (1972–81) of four measures of response (integral primary production, maximum volumetric primary production, Chl *a* concentration, and algal biomass) related to three P input variables (percent point source, point-source loading, and total loading). Correlation coefficients are for Belleville station data in the upper left corner of each panel and for Conway data at lower right. Lines are shown only for significant regressions.

important overall, both having very low coefficients of variation through 10 yr, 3.4% for radiation and 2.3 and 5.1% for temperature at the Belleville and Conway stations, respectively. At Belleville, flushing rate and P loading were most important; r^2 was 62% for Chl *a*, 31% for algal biomass, and 49% for integral primary production. Adding depth, radiation, and temperature gave r^2 values of 90, 35, and 79% for Chl *a*, algal biomass, and production. Results for the lower bay at Conway were poorer; only 60% of variability in Chl *a*, 25% in algal biomass, and 51% in integral primary production were accounted for by the five variables, with P loading and flushing rate being the most important independent variables.

Dissolved Oxygen

Significant oxygen depletion occurs in two time scales, in days or diurnally in the shallow upper bay and seasonally in the lower bay. Depletion to 1 mg · L^{-1} has been observed for brief periods in the upper bay and to 3–5 mg · L^{-1} by late summer in the lower bay. Pronounced oxygen depletion has been observed in the upper bay during occasional calm periods for many years (McCombie 1966; Minns and Johnson 1986), a product of high phytoplankton density and short-term periods of calm weather. Any reduction in algae should reduce the depletion rate in the upper bay but not necessarily the amplitude and certainly not the duration of oxygen depletion which are determined by weather events. A rigorous analysis of continuous data would be required to determine year-to-year trends. Regular weekly observations are inadequate. In the middle bay, thermal stratification during calm periods tends to produce oxygen depletion but the rate is subject to the extent of lower bay water intrusions.

During calm periods the oxygen concentration is higher in deep water, when much cooler water temperature indicates the intrusion of lower bay water, which demonstrates the ameliorating effect on oxygen depletion of these intrusions on the middle bay (Jackson 1976). There has been no obvious trend in oxygen deficits in lower Adolphus Reach and no link has been established between oxygen depletion and eutrophication of the bay (Minns and Johnson 1986).

Qualitative Changes in Phytoplankton and Macrophytes

Nicholls et al. (1986) compared phytoplankton species numbers before and after P removal at waste treatment plants and described the decrease in diatoms and blue-green algae and increase in chrysophytes. Their "*F*" index (sum of Cryptophyceae and Chrysophyceae divided by bloom-forming Cyanophyceae) increased from 1972–77 to 1978–81, indicating a greater proportion of algae suitable as food for zooplankton filter-feeders. The bloom periods of dominant taxa, such as *Stephanodiscus astraea*, *Melosira granulata*, *Anabaena* spp., and *Aphanizomenon* spp., became shorter in duration after 1977. These responses were correlated with declining P concentration, although nutrient interrelationships (P, N, Si) with phytoplankton community succession are complex (Nicholls et al. 1986). They speculated that the observed increase in the N:P ratio since 1977 was not sufficient to precipitate a major shift away from N-fixing blue-green algae. Further, P-loading reduction may lead to a sufficient surplus of inorganic N to remove any advantage now held by N-fixers.

No resurgence in macrophytes has been noted, in either mean biomass or towards or away from eutrophically adapted plants (Crowder and Bristow 1986).

Synthesis Using Models

General Considerations

The Bay of Quinte represents two atypical applications of the earliest P response models which related P loadings and mean depth to trophic state (Vollenweider 1968). First, the upper bay circulates continually, with only brief periods of thermal stratification, and it has a high flushing rate. The opposing effects of recirculation and removal by flushing of nutrients and algae, promoted by factors such as wind characteristics, regional climatology, and lake level which may be unrelated in real time, create a complex application of P-loading models. The importance of flushing rate was addressed by Dillon (1975), Dillon and Rigler (1974), and Vollenweider (1976). Degree of P retention is important in determining degree of eutrophy, but there likely are many poorly understood factors which influence the P-retention coefficient. Two of these, which are very relevant to Quinte studies, are the extent of macrophyte communities and the integrated effect of factors such as wind fetch and lake morphometry which affect the potential for mobilization of nutrients. An attempt will be made to incorporate the influence of macrophyte abundance on P retention in an extension of the Dillon–Rigler model. In Quinte studies, P concentration has been very closely related to algal abundance and production (as in many other studies), which makes it a useful bridge from P-loading models to responses by primary producers.

The second model application is to the lower bay, which has most of the characteristics of a temperate, dimictic lake, to which P-loading models have been most successfully applied, with the significant exception of large-volume intrusions of Lake Ontario water. In the May–September period this input is through the hypolimnion of the lower bay and it is mixed in the middle bay with outward flowing upper bay water. Lake Ontario P concentrations were consistently lower than upper bay outflow concentrations, 22 $\mu g \cdot L^{-1}$ compared with 60 $\mu g \cdot L^{-1}$ through 1972–81, although both input P concentrations declined during the period. Lower bay behaviour is probably different from upwelling because of the major influence of intrusions on increasing flushing rate and relatively lower P concentrations than those which accumulate in the hypolimnion of a lake of similar productivity. Therefore, the water volume and P contributed by intrusion of lake water were considered as inputs, in the same way that river inputs were considered in the upper bay model. Sodium ion concentrations were used to estimate the volume of lake water relative to upper bay water outbound through the epilimnion of the lower bay.

Limnological conditions in the upper and lower bays may not be closely related because the intrusion of lake water usually comprises the larger proportion of water entering the lower bay, especially during the summer months (while none enters the upper bay). Month-by-month comparisons (May–September) of 10 yr of data on P concentration in upper and lower bays showed no correlation in low-flow months (June–September) but strong correlation in May when flows were greater. Results using Chl *a* were the same.

Upper Bay Model

In the upper bay model, P concentration was estimated from P-loading rate, mean water depth, flushing rate, and P retention using a formulation developed by Dillon and Rigler (1974) and tested with data from lakes of the Haliburton Kawartha region of southern Ontario. Chl *a* concentration was determined using empirical relationships with P concentration. Macrophyte abundance was estimated from the photic zone depth based on Chl *a*–light extinction relationships. P retention was estimated from macrophyte abundance. Values of P retention provided feedback to the P concentration equation. Algal biomass could have been used in place of Chl *a*, but close correlation of the two variables indicated that results would be similar. Average May–October values of the variables were calculated for each year of the period 1916–81.

P concentration was predicted by the Dillon–Rigler model as

$$[P] = L(1 -R)/\bar{z} .\rho$$

with [P] in milligrams per cubic metre (micrograms per litre), P loading rate L in milligrams per square metre per unit time, mean depth $\bar{z}$ in metres, and flushing rate ρ for time t (153 d in the upper bay model); R is the P-retention coefficient. P loadings and flushing rates were available for the period 1916 to present (Minns et al. 1986). Lake Ontario water levels were converted to mean depths of the upper bay. Values of R were the result of calculations made in the balance of the model, to be described subsequently.

The equations for predicting Chl *a* concentration (C) from P concentration and the light extinction coefficient ε from Chl *a* are as follows:

$$C = 0.331[P]^{1.042}$$

$$\varepsilon = 0.3902 + 0.0506C.$$

The area of macrophytes was estimated from current understanding of the relations among phytoplankton density, light attenuation, and distribution of macrophytes with depth. Data provided by A. Crowder and P. G. Sly (pers. comm.), relating depth of significant macrophyte standing stock (Z_v) to Secchi values (Z_s), satisfied the function $Z_v = (Z_s)^{1.3}$. Compensation depth Z_c, defined as the depth of 1% of incident light (i.e.

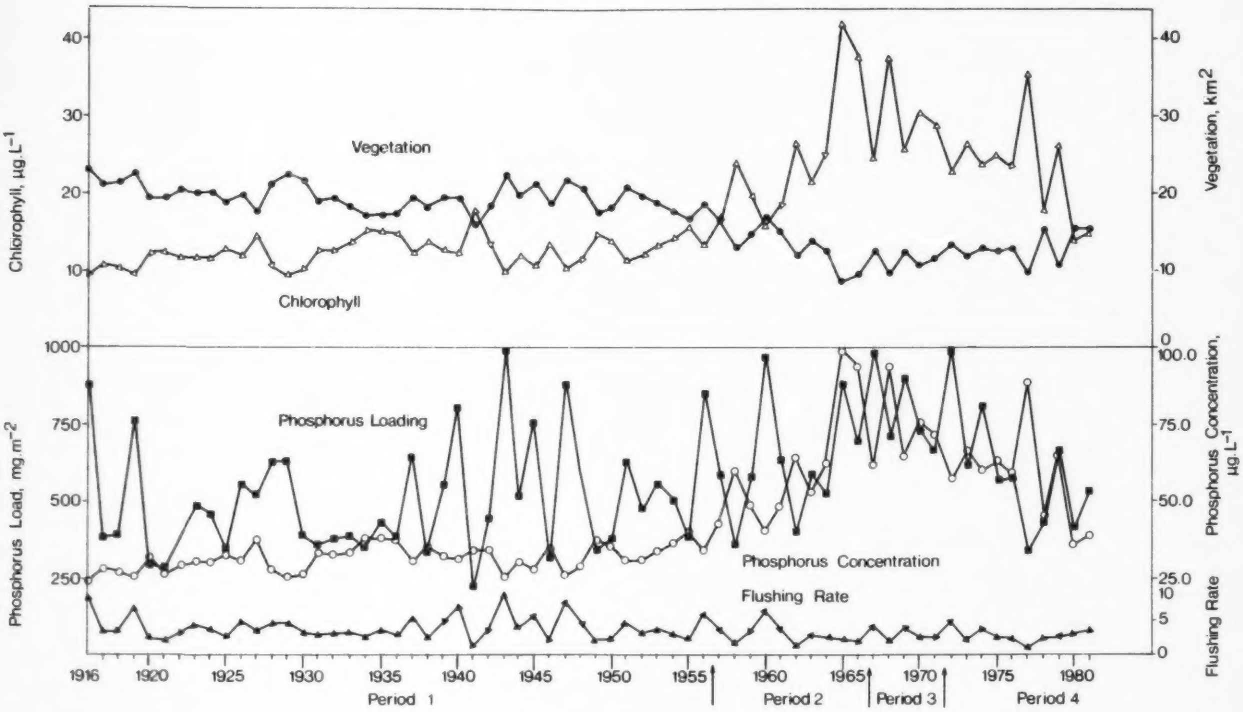

FIG. 3. Input variables for the upper bay model shown here are total P loadings and flushing rate. Output variables shown are P concentration, Chl *a* concentration, and coverage of the upper bay by macrophyte beds. The four periods shown along the time axis are described in the text.

4.605/ε where ε is the light attenuation coefficient per metre), was related to Z_s by the equation $Z_s = 0.411 + 0.307Z_c$ ($r = 0.963$) using Quinte cruise data. Therefore, $Z_v = (0.411 + 0.307Z_c)^{1.3}$, which permitted estimation of the maximum depth of distribution of significant macrophyte standing stocks (other factors being suitable) in relation to ε. Area vegetated was obtained using an area–depth function, with a further consideration that only one half of the upper bay has sufficient sediment and shelter for macrophytes (Crowder and Bristow 1986).

Assumptions about P retention in the upper bay are that macrophytes determine retention in proportion to the fraction of suitable substrate that they occupy within a range of zero (no macrophytes) to a probable value of R_{max} when peak abundance occurred. Modeled values of R for each year were derived as

$$R = R_{max} \cdot \text{Area vegetated (km}^2\text{)}/67.5\ \text{km}^2$$

where 67.5 km^2 is the area of the upper bay estimated to be suitable for macrophytes with adequate sediment and shelter. The value for R_{max} was adopted from a lake of similar morphometry, with P loadings similar to early Quinte loadings and natural abundance of macrophytes. Rice Lake, upstream in the Kawartha Lake–Trent River system, met these criteria; it has a published R of 0.46 (Ontario Ministry of the Environment and Ontario Ministry of Natural Resources 1976).

This model appears to oversimplify the macrophyte–algae interaction, considering only competition for light (as opposed to nutrients, for example). However, the abundance of macrophytes affects the value of R positively, which acts to decrease P concentration in the Dillon–Rigler model. Therefore, macrophytes reduce the flow of nutrients to algae, because nutrients retained in recent sediments in macrophyte beds are less available by resuspension to phytoplankton (and, presumably, more available to macrophytes). It seems reasonable that a fundamental impact of macrophytes on algae would be in maximizing sedimentation and R, while the main impact of algae on macrophytes would be shading, assuming that nutrient-enriched sediments make competition for new nutrient inputs much less important to macrophytes.

This model provides one means to examine the hypothesis of catastrophic decline in macrophytes suggested by Minns et al. (1986) with a combination of increased P loadings and decreasing macrophytes, depth, and flushing rates. The effect of increased P loading, which increases P concentration in the model directly, accelerates the increase in phytoplankton because of the reduction in R as macrophytes decrease. Decreased depths and/or flushing rates also favour phytoplankton relative to macrophytes by increasing P concentration. Lower than average depths and flushing rates often occur together; this was the case in 25 of the 33 possible co-occurrences during the 1916–81 period.

Inputs to the model included May–September P loadings, flushing rates, upper bay mean depth, and initial values for R of 0.45 for 1916 and 0.45 for R_{max}. Outputs included P concentration, Chl *a* concentration, and area occupied by macrophytes (Fig. 3). Modeled trends may be subdivided into four periods: 1916–56, a 41-yr period of fluctuating, mostly good environmental quality; 1957–66, a 10-yr period of accelerating deterioration; 1967–71, a 5-yr period of continuing poor environmental quality; 1972–81, a 10-yr period of gradual improvement.

The 1916–56 period was characterized by high variability in P loadings but relative uniformity in Chl *a* and area occupied by macrophytes. Although total P loadings were often high during the 1916–56 period, modeled P concentrations fluctuated between 25 and 40 µg · L^{-1} and were considerably influenced

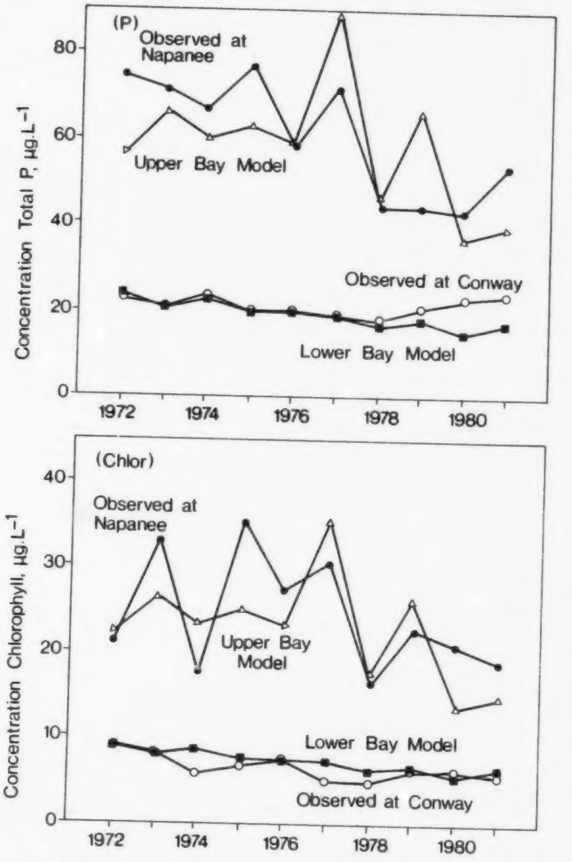

FIG. 4. Comparison of P (upper panel) and Chl *a* (lower panel) concentrations predicted by upper bay and lower bay models with concentrations observed at the Napanee and Conway stations, near the outlets of the upper bay and lower bay, respectively.

by flushing rate. For example, low flows in the early 1930's produced P concentrations that were among the highest in this first period. Chl *a* concentrations varied from 10 to 15 $\mu g \cdot L^{-1}$ with only three small departures, while the area of macrophytes varied to a small extent around 20 km^2. That is, within the one-half area of the upper bay with sufficient sediment and protection, about 30% received sufficient radiation to grow macrophytes. The *R* values averaged about 0.15. Although total P loadings and flushing rates varied almost as much as in later periods, their effects on P concentration and Chl *a* offset one another and contributed to stability in the primary producer system.

Over the next 10 yr, 1957–66, with accelerating point-source P loadings, P concentrations rose toward 100 $\mu g \cdot L^{-1}$ even though the total P loadings were similar to those during earlier years, especially the previous 20 yr, 1937–56. Chl *a* concentrations usually exceeded 20 $\mu g \cdot L^{-1}$ and reached 43 $\mu g \cdot L^{-1}$ in 1965 (Fig. 3). Macrophytes, in terms of area occupied, declined to about one half of their former abundance by 1965. The most rapid change appears to have occurred from 1962 to 1966, which was a 5-yr period with the lowest consecutive series of flushing rates at any time during the 66 yr modeled.

During the period 1967–71, P concentrations remained high and P loadings were more uniformly high than in previous periods. Higher flushing rates in some years probably offset the continuing high point-source P loadings. P and Chl *a* concentrations oscillated about 75 and 30 $\mu g \cdot L^{-1}$, respectively.

A trend towards improved water quality was evident from 1972 onward during the last period, especially after P removal at waste treatment plants in 1977. Three of the four last years had modeled P concentrations of less than 50 $\mu g \cdot L^{-1}$ and Chl *a* concentrations of less than 20 $\mu g \cdot L^{-1}$, representing a decline to concentrations estimated for several scattered years in the 1916–56 period, particularly in the 1930's and 1950's.

The overall trends in P concentrations and Chl *a* predicted by this model appear to be very closely related to trends in calculated sewage and detergent P inputs calculated by Minns (1986b) based on population, type of treatment, and detergent use. The highest levels of Chl *a* and P in water coincided with the 1962–66 period of lowest flushing rates, which compounded the effects on environmental quality of the steep, linear increase in sewage and detergent P inputs which took place through 1952–70. If there had been average flushing rates during that period, Chl *a* concentrations probably would have been no greater than 75% of values calculated using the real, lower flushing rates. Mean depth was also lower during that period but its contribution to higher P and Chl *a* concentrations was considerably less important.

Model predictions were compared with observations on P and Chl *a* concentrations, area vegetated by macrophytes, and calculated values of *R* from field studies carried out during the period 1972–81. Comparison of modeled P and Chl *a* concentrations with those observed at Napanee, the "outlet" station in the upper bay, showed good agreement, although the individual year predictions were sometimes different (Fig. 4).

There was also good agreement between predicted area occupied by macrophytes and that observed by Crowder and Bristow (1986). They observed an area of 6.27 km^2 with significant standing stocks of submerged and floating-leaved macrophytes, primarily in the upper bay, or about 9% of the area suitable for macrophytes. This was likely the minimum abundance of macrophytes in recent time. The minimum area of macrophytes predicted by the model, at the time of highest Chl *a* and lowest water transparency, was approximately 9 km^2 and 13% of suitable area occupied. However, the model predicted an increase in macrophytes during 1978–81 as phytoplankton decreased. Field observations (A. Crowder, pers. comm.) indicate that expansion of macrophyte beds has not yet occurred. Anecdotal evidence suggested that growth of submerged macrophytes increased during the 1950's and 1960's (Crowder and Bristow 1986), but the model predicted a decrease in area vegetated as transparency declined. These observations may not be contradictory if macrophytes had developed maximum areal standing stocks at the time of greatest point-source P inputs, even though their distribution had been restricted. Minns et al. (1986) calculated *R* values for the upper bay during May–October of each year of the period 1967–81. The average value was 0.01, but there was considerable variability, particularly after 1976 when export was suggested by some high negative values of *R* in some years. The average for the period 1967–76 was 0. The model predicted an *R* value of 0.06 at the point of minimum area occupied by macrophytes.

Lower Bay Model

The Dillon–Rigler model was used to estimate P concentration from annual data on P loading, mean depth, flushing rate, and P retention. Chl *a* was predicted from P concentration. In this case also, algal biomass could have been used but results would have been similar. The Lake Ontario intrusion was treated

TABLE 1. Na^+ concentrations used in determination of ρ L (stations: N, Napanee; Ge, Glenora epilimnion; Ch, Conway hypolimnion) and annual loading rates of P and flushing rates attributable to upper bay inputs (B) and Lake Ontario inputs (L) for the lower bay.

	Na^+ Concentration ($mg \cdot L^{-1}$)			Flushing rates		Loading rates ($g \cdot m^{-2} \cdot yr^{-1}$)	
Year	N	Ge	Ch	ρ^B	ρ^L	L_B	L_L
1972	3.3	7.8	11.0	4.56	6.4	6.10	3.76
1973	4.7	9.5	11.5	4.29	10.3	5.29	6.31
1974	4.0	8.8	11.5	4.29	7.6	5.81	4.66
1975	4.5	9.7	12.0	3.35	7.6	3.81	4.28
1976	4.4	9.2	11.7	3.92	7.5	4.20	4.23
1977	6.4	10.3	11.8	2.92	7.6	3.42	4.10
1978	4.8	9.3	11.1	3.93	9.8	3.94	4.56
1979	3.4	9.2	11.6	4.44	12.2	7.11	4.32
1980	4.6	8.9	11.3	4.13	7.4	3.13	3.44
1981	5.0	9.0	11.7	4.00	5.9	3.81	2.74

as an additional input of P and contributor to the value of ρ. This influx actually originates in Prince Edward Bay and the North Channel, but for simplification, it is called Lake Ontario water.

The contribution of the Lake Ontario influx to flushing rate in the lower bay was calculated as follows. Hypolimnion water at Conway was assumed to be predominantly Lake Ontario water. Na^+ concentrations averaged 11.5 $mg \cdot L^{-1}$ in Conway hypolimnion water and 4.5 $mg \cdot L^{-1}$ in upper bay water at Napanee, with low annual variability in each case (Table 1). The coefficient of variation was 3% at Conway and 19% at Napanee. The middle bay mixes most of the time, and therefore, outbound surface water at Glenora should be representative of the two mixed inputs. Using data on Na^+ concentrations in Glenora surface water, the proportions of the two inputs, upper bay and lower bay hypolimnion waters, were determined. Lake Ontario inflows were calculated from known upper bay flows and their relative proportions (Table 1). The estimated flushing rates contributed by lake inflows varied through the 10 yr from 5.9 to $12.2 \cdot yr^{-1}$, but they were always greater than the flushing rates of the lower bay attributable to upper bay water, by 1.4–2.7 times. This analysis was a simplified version of the calculations made by Minns et al. (1986), but the results were comparable. The average contribution to lower bay flushing rates by Lake Ontario intrusions was $8.2 \cdot yr^{-1}$ here and $8.9 \cdot yr^{-1}$ in the latter study.

P concentrations in Lake Ontario were applied for each year to the estimated lake water inflows to calculate P loading from this source. P concentration in the lake declined from 24–25 $\mu g \cdot L^{-1}$ to 18–19 $\mu \cdot L^{-1}$ during the 10-yr period 1972–81 (Great Lakes Water Quality Board 1981). P loading to the lower bay from the upper bay and from Lake Ontario are similar (Table 1) but the flushing rate effect is greater for lake water intrusions. Retention of P above the lower bay is low, and, in fact, there may be a small negative *R* for the upper bay in recent years (Minns et al. 1986). For purposes of lower bay modeling, negligible retention or export above the lower bay was assumed.

The average value of *R*, estimated by Minns et al. (1986) for the lower bay, was 0.28. A simpler estimator of *R* is the relative change in P concentration between the Glenora and Conway stations. This averaged 0.3 through 1972–81 and varied from 0.2 to 0.4 with no detected correlation with flushing rate. However, use of a value of *R* independent of the Quinte data base on P would be preferable. Some *R* values were available for lakes with similar flushing rate and morphometry in eastern Ontario. Dillon and Rigler (1974, tables 1 and 2) gave *R* values of 0.27 for Eagle-Moose Lake, 0.37 for Maple Lake, and 0.40 for Twelve Mile–Boshkung Lake (average 0.35). Therefore, an *R* value of 0.35 was used in the lower bay model.

Estimates of P concentration and Chl *a* were made only for the 1972–81 period for which data were available to estimate contributions of lake water intrusions on P loading and ρ. These estimates permit assessment of the validity of assumptions about lower bay limnology. If good agreement occurred between modeled observed P and Chl *a* concentrations during 1972–81, predictions about earlier water quality conditions in the lower bay could be attempted, recognizing that these would be very general. Both modeled and observed Chl *a* declined slowly through the 1972–81 period in the lower bay (Fig. 4), from about 8–9 to 6–7 $\mu g \cdot L^{-1}$. The model indicated a general decrease in P concentration, while field data showed a decline from 23 to 18 $\mu g \cdot L^{-1}$ in 1978 followed by an increase to 24 $\mu g \cdot L^{-1}$ in 1981. Agreement was sufficiently close to allow speculation about earlier conditions.

General estimates of P concentration and Chl *a* in the lower bay in 1916–56 were obtained using average values of ρ for 1972–81 and calculated P loadings. Loadings of P to the lower bay were calculated from upper bay and Lake Ontario P concentrations and their respective contributions to ρ. Values of ρ were $4 \cdot yr^{-1}$ attributable to upper bay inputs and $8 \cdot yr^{-1}$ attributable to lake water intrusions. P concentration in the upper bay was 30 $\mu g \cdot L^{-1}$ in 1916–56, estimated in the upper bay model, compared with an average of 66 $\mu g \cdot L^{-1}$ in six years before the P-control program was initiated. The P concentration in Lake Ontario averaged 24 $\mu g \cdot L^{-1}$ in the mid-1970's and approximately 12 $\mu g \cdot L^{-1}$ in the early period (Chapra 1977). Estimated P concentration and Chl *a* in the lower bay for the earlier period were 10 and 4 $\mu g \cdot L^{-1}$, respectively. The estimated relative change in P concentration between periods was 2.2 times, the same as the relative change in the upper bay. The estimated change in Chl *a* was from 4 to 8 $\mu g \cdot L^{-1}$ (2.0 times) for the lower bay, which is similar to the relative change in the upper bay, from 12 to 26 $\mu g \cdot L^{-1}$ (2.2 times).

Critical P Loading

In the first nutrient budget published on the Bay of Quinte (Johnson and Owen 1971), an attempt was made to place river (low concentration, high volume) and point-source (high concentration, low volume) inputs in proper perspective by calculating net inputs for every source. Net input was the amount of P contributed to the bay in excess of P displaced at the bay mouth

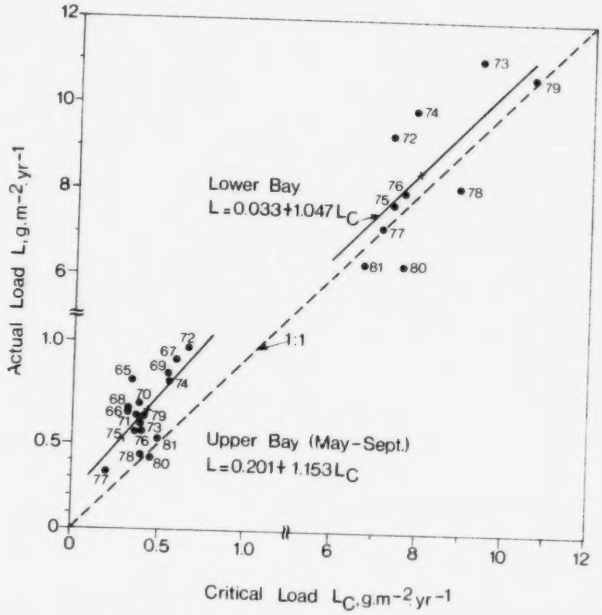

FIG. 5. Comparison of actual P loadings to upper and lower bays with critical loadings calculated for each of the years indicated. Critical load formulation is that of Vollenweider (1976).

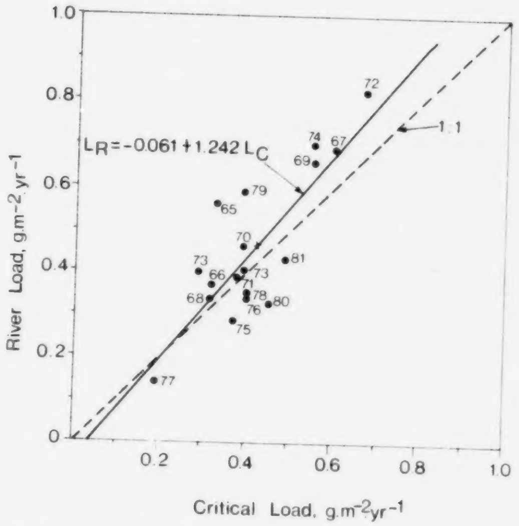

FIG. 6. River P loadings only are compared with critical P loadings calculated for each of the years plotted for the upper bay using the equation of Vollenweider (1976).

in an equal volume of water. This was an implicit formulation of hydraulic load. Vollenweider's (1976) critical load expression is another approach to the consideration of P loadings in relation to associated hydraulic loads:

$$L_C = [\mathrm{P_{sp}}] \cdot q_s\ (1 + \sqrt{\bar{z}/q_s})$$

where $q_s = \bar{z}/T_w$ ($\bar{z}$ is mean depth and T_w is turnover time of water) and $[\mathrm{P_{sp}}]$ is an empirical constant representing incipient cultural eutrophy, a spring P concentration of 10–20 $\mu g \cdot L^{-1}$.

In the Bay of Quinte, where hydraulic load varies widely from year to year, each year's actual load may be expected to affect water quality to a degree relative to the critical load for that year. Similarly, in the upper bay, a May–September real load probably has an effect relative to the critical loading for that period, in view of the conclusion that late winter and early spring loadings may have little effect at all on environmental quality during the following growing season.

To obtain values of $[\mathrm{P_{sp}}]$ appropriate for the Bay of Quinte, it was assumed that the critical load actually occurred in the 1916–40 period when water quality probably was relatively stable and just before the onset of the variety of problems typical of cultural eutrophy. At a whole-bay annual loading of 0.84 $g \cdot m^{-2} \cdot yr^{-1}$, $[\mathrm{P_{sp}}]$ equalled 21.6. With appropriate allocation of part of this load to the May–September period to the upper bay only, $[\mathrm{P_{sp}}]$ equalled 27.1.

Critical loadings to the upper bay were calculated for years for which river and total loadings were measured, 1965–81. Calculation of critical loadings to the lower bay was restricted to the period 1972–81 when lake water intrusions were quantified. Critical loadings to the upper bay during May–September were highly variable (Fig. 5), as low as 0.19 $g \cdot m^{-2} \cdot yr^{-1}$ (1977) to as high as 0.67 $g \cdot m^{-2} \cdot yr^{-1}$ (1972), although in most years critical loadings were between 0.3 and 0.5 $g \cdot m^{-2} \cdot yr^{-1}$. Critical loadings for the lower bay varied from 6.7 to 10.6 $g \cdot m^{-2} \cdot yr^{-1}$. These and measured P loading values are not directly comparable with upper bay loadings because of a different time base. However, the actual P loadings to both upper and lower bays exceeded their respective critical loadings in the majority of years.

River loadings to the upper bay (Fig. 6) were approximately equal to critical loadings to the upper bay. The slope of the regression of river loadings on critical loadings was very close to 1. However, in all years 1965–70, river loadings exceeded critical loadings, and after 1974 all river loadings except for 1979 were less than critical loadings. This analysis suggests that river loadings alone would have been sufficient to produce conditions of cultural eutrophy during 1965–74.

There was a decreasing trend in values of $L{:}L_C$ as P control measures were implemented. The earliest years in the upper bay series, 1972–74, had the highest values of the ratio $L{:}L_C$. May–September P loadings to the upper bay were about 50% greater than critical loadings until after P removal, when 1978, 1980, and 1981 $L{:}L_C$ values were close to 1. During the period 1965–81, $L{:}L_C$ values for the upper bay decreased from 2.45 to 0.94 primarily as a result of the overall P-removal program. Similarly, in the lower bay, values of $L{:}L_C$ decreased to near 1 in most years from 1975 to 1979 and to below 1 in 1980 and 1981. It is not surprising that correlations between the ratio $L{:}L_C$ and limnological variables were considerably stronger than when the total load L was used (Table 2) because of the recognized influence of flushing rate on bay productivity.

Discussion

Eutrophication of the Bay of Quinte was the result of steadily increasing point-source P loadings, aggravated at times by low water flows through the bay. Increasing point-source P inputs after 1950 appear to be closely related to modeled estimates of P concentration and Chl *a*. However, the 5-yr period, 1962–66, of below average river flows (and flushing rates) likely accelerated deteriorating environmental quality. This period is apparently when the "catastrophic decline" in macrophytes, suggested by Minns et al. (1986), occurred. The model simulation suggests more gradual change than what might have actually occurred.

Flow regimes are manipulated in summer on the Trent River system to maintain navigable levels in lakes, possibly at the

TABLE 2. Correlation coefficients ($n = 10$, 1972–81) between limnological variables and $L:L_c$ and L for the upper bay (May–September) and lower bay (annual). Probabilities on significance test: * <0.10, * * <0.05, * * * <0.01.

Dependent variable	Correlation coefficients with $L:L_c$	Correlation coefficients with L
Upper bay		
Extinction coefficient	0.674* *	0.221
Chl *a*	0.551*	−0.091
Phytoplankton density	0.545*	0.316
Integral primary production	0.679* *	0.228
A_{max}	0.765* * *	0.248
[P]	0.684* *	0.276
Lower bay		
Extinction coefficient	0.449	0.318
Chl *a*	0.534*	0.344
Phytoplankton density	0.488	−0.031
Integral primary production	0.705* *	0.410
A_{max}	0.912* * *	0.516*
[P]	0.196	0.007

expense of water quality in the Bay of Quinte. The Trent River contributes about 70% of water inputs to the bay. Also, the upper bay model suggested that low flow during the period 1930–36 was responsible for a continuous year-to-year increase in Chl *a*. This was a period when water treatment at Belleville was made difficult for the first time because of filter clogging and poor water taste. Therefore, it will be necessary for environmental management agencies to consider flow regulation together with P-removal programs as part of future management strategy. There has been no detailed analysis done to date on the possible effect of flow manipulation on environmental quality in the Bay of Quinte by comparative simulations using regulated and unregulated flows.

Point-source P control has been successful in reducing ambient P concentrations in most parts of the Bay of Quinte to levels characteristic of the early 1950's, and desirable changes in environmental quality have occurred throughout the bay. Observed phytoplankton abundance and production in the upper bay declined roughly in proportion to the decline in P concentration through the period of P control. P concentrations declined slightly at Glenora but no change was detected at Conway in the lower bay, although all measures of phytoplankton abundance and production have decreased. Intensified sampling and analysis of data may show a statistically significant decrease in P concentration at Conway. At this time, however, the improvement in environmental quality at Conway is not explained by declining P concentration.

The problem of recycling of P by resuspension of sediments and mixing of interstitial water in the upper bay, shown by Wright (1976) to be a storm-event phenomenon, apparently did not negate efforts of the nutrient-removal program. Obviously this is a feature of upper bay limnology which promotes high phytoplankton productivity. However, its impact on phytoplankton may be no more than the effect of change in relative abundance of macrophytes which, among other factors, influence resuspension and compete for nutrients. The favourable response in environmental quality suggests that temporarily resuspended P may be less conducive to sustained high phytoplankton production than continuous inputs of available P which declined sharply after 1977. Resuspension of P must be less important than new point-source inputs in maintaining available P in the photic zone, because Robinson (1986) showed a reduction in average soluble reactive P following 1977. However, the significance of shallow, nutrient-enriched sediments in slowing recovery of water quality continues to be a central limnological question in the study (Minns 1986b).

Models of the type used here might be considered naive because they completely ignore possible effects of trophic level interactions on the phytoplankton community (Shapiro 1980). Significant changes in the fish community have occurred, with the recent decline of the alewife (*Alosa pseudoharengus*) and the white perch (*Morone americana*) and increase in walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) reported by Hurley (1986). Changes in the fish community may alter zooplankton–phytoplankton relations to cause shifts in abundance of primary producers not predicted by these simple models. However, there is no evidence to date that this has occurred at the zooplankton–phytoplankton level, as indicated by research on zooplankton and algae (Cooley et al. 1986; Nicholls et al. 1986) and by good agreement here of model results and observations. When planktivorous fish were abundant, low zooplankton populations and high algal standing stocks might have been expected. With the decline in planktivorous fish, zooplankton might have increased and algae declined. However, the main species of zooplankton either decreased or remained at about the same population level when alewife and white perch numbers declined. Perhaps these trophic interaction effects operate on only part of the algal community and are damped out in the overall response. K. H. Nicholls (pers. comm.) suggested that many bloom-forming algae in the Bay of Quinte are sufficiently large forms that their numbers may not be affected significantly by zooplankton numbers. Linkages between primary producer dynamics and secondary production, especially fish, continue to be elusive.

Expectations for environmental improvement should be tempered by what we know or by what can be inferred about earlier trends. The upper bay and lower bay models suggested that P and Chl *a* (and, presumably, phytoplankton density and production rates) approximately doubled during the 15-yr period 1957–71 and that pre-1950 trophic conditions of the upper bay must have bordered on a eutrophic state, with modeled concentrations of Chl *a* of 10–16 $\mu g \cdot L^{-1}$ and 25–40 μg total $P \cdot L^{-1}$. These concentrations occurred in the western basin of Lake Erie, the barometer of cultural eutrophy, during the period 1970–80 (Great Lakes Water Quality Board 1981). In fact, problems with municipal water treatment at the Bay of Quinte began as early as the 1930's. Also, calculated critical loadings for the Bay of Quinte were close to the river loadings, suggesting again that the upper bay would border on the eutrophic state without point-source P inputs to the bay. Paleolimnological work on Glenora station sediment cores showed that deforestation in the watershed and poor agricultural practices resulted in rapid change toward a moderate degree of eutrophication by the early 1850's (Stoermer et al. 1985; Warwick 1980). Consequently, a realistic goal would be to achieve conditions typical of the years 1916–30 (as suggested by this simulation) and to maintain them. This probably would be a tolerable level of environmental quality, but the pre-1930 conditions should not be misrepresented as a return to the natural trophic state of the bay or any state described as better than moderately eutrophic. To maintain relativity the worsening condition of the bay during 1957–71 could be defined as advancing hypereutrophy.

Continuous vigilance will be required to hold point-source P inputs to current levels, and reductions in per capita inputs will be necessary. River inputs should decrease slightly with improvements in land management. However, no large reduction in P export can be expected in these large drainage basins where intensive row-crop agriculture is not dominant and where retention of P in large lakes diminishes the effects of nutrient removal at source. All non-point sources of P should be sufficiently controlled that river P concentrations are not increased. Summer flow regulation of rivers, particularly the Trent River, should be recognized as potentially part of the remedial strategy.

The models employed in this study should be useful in consideration of present and future nutrient management possibilities. Simulation of the responses to factors not under management control would allow environmental quality parameters to be considered as a range in values. Refinement of management models to deal with backflow of nutrients to the water column from sediments, with declining concentrations in sediments, should be important (Minns 1986b). The concept of net input (Johnson and Owen 1971) may continue to be useful in comparing the relative contributions of various point and non-point P inputs to enrichment of the bay.

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References

CHAPRA, S. C. 1977. Total phosphorus model for the Great Lakes. J. Environ. Eng. Div., Proc. Am. Soc. Civ. Eng. 103: 147–161.

COOLEY, J. M., J. E. MOORE, AND W. T. GEILING. 1986. Population dynamics, biomass, and production of the macrozooplankton in the Bay of Quinte during changes in phosphorus loadings, p. 166–176. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

CROWDER, A., AND M. BRISTOW. 1986. Aquatic macrophytes in the Bay of Quinte, 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

DILLON, P. J. 1975. The phosphorus budget of Cameron Lake, Ontario. The importance of flushing rate to the degree of eutrophy of lakes. Limnol. Oceanogr. 20(1): 28–39.

DILLON, P. J., AND F. H. RIGLER. 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. J. Fish Res. Board Can. 31: 1771–1778.

GREAT LAKES WATER QUALITY BOARD. 1981. Report on Great Lakes water quality. Appendix — Great Lakes surveillance. International Joint Commission, Windsor, Ont. 174 p.

HURLEY D. A. 1986. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

JACKSON, M. B. 1976. Water quality in the Bay of Quinte prior to phosphorus removal at sewage treatment plants. Ontario Ministry of the Environment, Toronto, Ont. 62 p.

JOHNSON, M. G., AND D. A. HURLEY. 1986. Overview of Project Quinte — 1972–82, p. 1–6. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec Publ. Fish. Aquat. Sci. 86: 270 p.

JOHNSON, M. G., AND O. C. MCNEIL. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–84, p. 177–189. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

JOHNSON, M. G., AND G. E. OWEN. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control. Fed. 43(5): 836–853.

MCCOMBIE, A. M. 1966. Some physical and chemical characteristics of the Bay of Quinte. Res. Rep. Ont. Dep. Lands For. 79(1): 1–XX.

MILLARD, E. S. 1986. Effect of light climate, photosynthetic capacity, and respiration on gross integral primary production and net primary production potential in the Bay of Quinte, Lake Ontario, p. 128–138. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

MILLARD, E. S., AND M. G. JOHNSON. 1986. Effect of decreased phosphorus loading on primary production chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

MINNS, C. K. 1986a. Total phosphorus loading to the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. A simple whole-lake phosphorus model and its application to the Bay of Quinte, p. 84–90. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

MINNS, C. K., AND M. G. JOHNSON. 1979. Temporal variation in the nutrient export of rivers during draining into the Bay of Quinte, Ontario, Canada. Water Resour. Bull. 15(4): 1061–1072.

1986. Temperature and oxygen conditions and oxygen depletion in the Bay of Quinte, Lake Ontario, p. 40–49. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

MINNS, C. K., G. E. OWEN, AND M. G. JOHNSON. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

NICHOLLS, K. H., L. HEINTSCH, E. CARNEY, J. BEAVER, AND D. MIDDLETON. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

ONTARIO MINISTRY OF THE ENVIRONMENT AND ONTARIO MINISTRY OF NATURAL RESOURCES. 1976. The Kawartha Lakes Water Management Study — Water quality assessment (1972–1976). 185 p.

ROBINSON, G. 1986. Water quality of the Bay of Quinte, Lake Ontario, before and after reductions in phosphorus loading, p. 50–58. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario.

Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Shapiro, J. 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes, p. 105–116. *In* J. Barica and L. R. Mar [ed.] Developments in hydrobiology. Vol. 2. W. Junk BV Publishers, The Hague, Boston, London.

Sly, P. G. 1986. Review of postglacial environmental changes and cultural impacts in the Bay of Quinte, p. 7–26. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Stoermer, E. F., J. A. Wolin, C. L. Schelske, and D. J. Conley. 1985. Postsettlement diatom succession in the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. 42: 754–767.

Vollenweider, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to phosphorus and nitrogen as factors in eutrophication. OECD Tech. Rep. DAS/CSI/68.27: 159 p.

1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53–83.

Warwick, W. F. 1980. Paleolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 115 p.

Wright, D. G. 1976. Wind induced regeneration of phosphorus from the sediments of the upper Bay of Quinte. M.Sc. thesis, University of Guelph, Guelph, Ont. 62 p.

Trophic Structure and Interactions in the Bay of Quinte, Lake Ontario, before and after Point-Source Phosphorus Control[1]

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Project Quinte data are used to test several hypotheses to explain the observed changes in the Bay of Quinte that occurred as nutrient loading increased up to the mid-1970s and as loads decreased after 1977. The nutrient hypothesis states that the bay condition is a direct result of excessive phosphorus inputs. The predation hypothesis states that changing predator-prey relationships result in the same conditions seen when phosphorus inputs are excessive. The succession hypothesis states that the condition of the bay ecosystem results when the orderly, directional stages of development are stressed by nutrient additions and other stress factors that surpass the resilience of the system. Each hypothesis partially explains the data, but transitions, especially in phytoplankton–zooplankton interactions, do not fit the hypotheses well. A size-spectrum model of biomass predicts that the biomass of small zooplankton is greater than expected, while that for small fish is smaller than expected. This model predicts that the transfer of biomass is being restrained and that the ecosystem is not at a steady state. The Bay of Quinte is compared with other areas in the Great Lakes Basin that receive less and more nutrients at the present time. Several guidelines are presented by which the rehabilitation of the Bay of Quinte, and other areas in the Great Lakes Basin, can be assessed.

On se sert des données du projet Quinte pour vérifier plusieurs hypothèses visant à expliquer les changements observés dans la baie de Quinte, qui se sont produits lorsque la charge de substances nutritives a augmenté jusqu'au milieu des années 70 et que les charges ont diminué après 1977. L'hypothèse faisant appel aux substances nutritives soutient que l'état de la baie est une conséquence directe d'apports excessifs de phosphore. L'hypothèse de la prédation soutient que les rapports changeants entre les prédateurs et les proies aboutissent aux mêmes conditions que celles observées lorsque les apports de phosphore sont excessifs. L'hypothèse de la succession soutient que les effets sur l'écosystème de la baie se font sentir quand les étapes ordonnées et directionnelles du développement sont accentuées par des ajouts de substances nutritives et par d'autres facteurs de stress qui surpassent la résilience du système. Chaque hypothèse explique particulièrement les données, mais les transitions, particulièrement dans les interactions entre le phytoplancton et le zooplancton, ne concordent pas très bien avec les hypothèses

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formulées. Un modèle de biomasse par gamme de taille prédit que la biomasse des petits organismes zooplanctoniques est plus grande que prévu, tandis que dans le cas des petits poissons, elle est plus petite que prévu. Ce modèle prédit que le transfert de la biomasse est limité et que l'écosystème n'est pas dans un état stable. On compare la baie de Quinte avec d'autres secteurs dans le bassin des Grands Lacs qui reçoivent actuellement moins et plus de substances nutritives. On présente plusieurs lignes directrices qui permettent d'évaluer la remise en état de la baie de Quinte et d'autres secteurs situés dans le bassin des Grands Lacs.

Introduction

The main purpose of this paper is to consider the applicability of a number of models that have been proposed to explain the behaviour of the Bay of Quinte ecosystem in response to changes in nutrient loading and in predator–prey interactions. An important element of any model is its ability to explain the observed events both in the years when eutrophication was increasing and also when eutrophication was decreasing.

Initially, Project Quinte was developed to test a "nutrient" hypothesis. This stated that the degraded condition of the Bay of Quinte ecosystem was a direct result of excessive inputs of phosphorus. Summer loadings were extremely high, especially from sewage treatment plants, at a time when flow rates were low (Johnson and Owen 1971). It was postulated that a reduction in point-source inputs would lower phosphorus levels and result in lower phytoplankton density and improved water clarity. These improvements would in some unknown manner be transferred to the higher trophic levels, and ultimately result in a return to a biotic assemblage similar to that present before phosphorus inputs became excessive. The rates at which changes would occur in the various trophic levels were the main factors to be studied.

A major difficulty with the "nutrient" hypothesis was the mechanism by which changes at the lower trophic levels would transfer to the higher trophic levels, and ultimately to the fish community. For this reason, the Project Quinte group cautioned those in the Ministry of Natural Resources responsible for fisheries management that coarse fish removal and hatchery-planting of game fish might be required to facilitate restoration after the initial reduction in phytoplankton biomass.

Another hypothesis, the "predator" hypothesis, states that the bay ecosystem is structured by predator–prey relationships that were severely distorted by the loss of certain key predators or predator assemblages in the eutrophication sequence. This hypothesis derives from observations of numerous authors on the effects of predators on the size distribution of prey items (Hrbáček et al. 1961; Shapiro et al. 1975; Andersson et al. 1978; Lynch and Shapiro 1981; Benndorf et al. 1984; Reinertsen and Olsen 1984; Shapiro and Wright 1984). Hurley and Christie (1977) extended this hypothesis to the fish community of the Bay of Quinte, which became dominated by stunted benthivores and planktivores when piscivore abundance declined. The piscivore decline was linked to the selectively deleterious effects of eutrophication. Christie and Scott (1985) analyzed the stunting effect among Bay of Quinte fishes and showed that growth patterns are controlled by predator–prey interactions that determine the degree of homeostasis in a community.

The "succession" hypothesis states that the events observed in the bay were a succession of transient steady states imposed by, at first, the increasing stress of phosphorus enrichment and, latterly, its relaxation. Odum (1969) said that ecosystem development was orderly, directional, and therefore, predictable. Stresses such as eutrophication, non-native species introductions, exploitation, and climate variations would retard the orderly development of the community and place it at a more immature stage. Holling (1973) saw ecosystem change as a result of the basic resilience of a system being overcome by stress that could not be absorbed. When this limit was passed, the system changed rapidly to a new level. In this case, persistence was the result of resilience, and successional stages observed in an ecosystem were the result of an orderly, predictable development.

In the final analysis, data from Project Quinte lend support to some aspects of each of the above models. In this paper the evidence for each model is presented. A further model based on the size-spectrum of biomass in the Bay of Quinte and developed by Minns et al. (1985) brings together features of both the "nutrient" and "predator" hypothesis. In this latest model, nutrients control the level of the total biomass of the system, but the degree to which a smooth biomass spectrum is achieved is determined by the slope of the biomass spectrum, trophic interactions, and perturbations such as fishery exploitation.

The approach used during Project Quinte was to compare and contrast conditions in the Bay of Quinte before and after phosphorus inputs from sewage treatment plants were substantially reduced. In order to observe conditions in an area that had not received the nutrient load that the Bay of Quinte had, West Lake, a nearby embayment of Lake Ontario which is morphologically and biologically similar to the upper Bay of Quinte, was used as an indicator of the condition in which the Bay of Quinte historically may have been. Other areas in the Great Lakes Basin that have become eutrophic are used to illustrate the position of the Bay of Quinte in the eutrophication sequence.

Assessment of the abiotic and biotic elements of the Bay of Quinte will be required on a continuing basis in order to effectively manage the bay ecosystem in the future. Several models are described in this synthesis which can be used to judge the degree of rehabilitation of the bay. The fact that some of these models are not quantitative illustrates the point that continued research is required.

The Bay of Quinte before Phosphorus Control

The degree of degradation of the Bay of Quinte ecosystem in the late 1960s has been largely inferred, since only anecdotal data exist from earlier times to measure the differences (Christie 1985). The long-term development of the bay with changes in climate and water levels are described by Sly (1986). The major trophic changes beginning 2000 yr ago have been documented from analysis of chironomid assemblages (Warwick 1980) and diatom associations (Stoermer et al. 1985).

The data on abundance and distribution of the biota which are available for the 1960 decade are cited by various authors in this volume (Nicholls et al. 1986; Johnson and McNeil 1986; Crowder and Bristow 1986; Hurley 1986a). A summary of phosphorus concentrations and the biomass of the major forms in each of the three major sections of the bay before phosphorus control (1972–77) is given in Table 1. The average

TABLE 1. Values for various parameters in the upper, middle, and lower sections of the Bay of Quinte for the May–October period in the pre-phosphorus (1972–77) and post-phosphorus (1978–82) control periods.

	Upper bay		Middle bay		Lower bay	
	1972–77	1978–82	1972–77	1978–82	1972–77	1978–82
Total phosphorus ($\mu g \cdot L^{-1}$)	60–78	43–48	45–53	36–41	19–33	17–28
Primary production rate ($mg\ C \cdot m^{-3} \cdot h^{-1}$)	185–197	100–118	132	94	45–80	33–59
Phytoplankton ($mm^3 \cdot L^{-1}$)	11.5–13.1	6.5–6.9	8.7	5.8	2.5–4.5	1.4–3.1
Zooplankton (μg dry weight $\cdot L^{-1}$)						
Cyclopoids	78.3–123.0	46.9–78.9	91.5	84.6	38.8–62.1	74.6–82.0
Calanoids	2.1–3.3	3.4–3.6	7.6	5.0	4.1–5.9	4.4–5.6
Cladocerans	291.7–300.9	219.5–279.3	205.8	257.1	50.0–125.5	78.8–163.6
Macrobenthos (g ash-free dry weight $\cdot m^{-2}$)	1.77	1.34	—	—	3.75–3.82	1.77–1.81
Macrophytes (g dry weight $\cdot m^{-2}$)	25.84[a]	25.84	25.84	25.84	25.84	25.84
Fish (kg wet weight $\cdot ha^{-1}$)	145.6	65.7	161.4	77.0	125.8	37.8

[a] Weighted mean, no location or year difference.

May–October total phytoplankton biomass was significantly correlated ($P < 0.001$) with average total phosphorus. Bloom-forming blue-green algae became dominant in the bay as phosphorus levels increased and formed floating accumulations that were not "food-chain functional" (Nicholls et al. 1986). Other dominant species, such as *Melosira* spp., were also substantially not food-chain functional. Maximum primary production rates in the upper bay (288–533 mg $C \cdot m^{-3} \cdot h^{-1}$) were among the highest recorded for temperate-climate lakes (Millard and Johnson 1986).

Cooley et al. (1986) showed that the bay was dominated by small cladocerans in the 1972–77 period. In fact, the total seasonal production of cladocerans was, on average, about 8000 $\mu g \cdot L^{-1}$ (dry weight) in the May–October period in the upper bay (Cooley et al. 1986). This represents some of the highest values found in freshwaters. In addition, cladocerans formed a gradient of decreasing seasonal production from the upper to the lower areas of the bay on a volumetric basis.

Benthic macroinvertebrate communities in the upper bay were dominated by a chironomid association which could persist during periods of reduced dissolved oxygen (Johnson and McNeil 1986). In the lower bay, conditions were more mesotrophic and the community association was of many sphaerid, oligochaete, chironomid, and crustacean species (Johnson and McNeil 1986).

Production of macroinvertebrates depended upon the rate of importation of utilizable energy which was less in the upper bay than in the lower bay (Johnson and Brinkhurst 1971). Oxygen depletions in the lower bay may have restricted the distribution of some macrobenthic forms.

The aquatic macrophyte community may have covered more than 20% of the bay area in the 1950s, but it covered only 14% of the total area by the 1970s (Crowder and Bristow 1986). Submerged macrophytes were limited to a 2 m depth in the upper bay and to 4 m toward the lower bay. Standing crop, species richness, and cover were particularly low in the Belleville–Big Bay area. *Myriophyllum spicatum* invaded the bay and became a dominant species during the years of advancing eutrophication.

Changes within the fish community were studied extensively after the 1950s, and the major impact of increasing nutrient levels was inferred to be the reduction of large piscivores and the ascendance of planktivores and benthivores (Hurley and Christie 1977). Reduced light transparency probably favoured the benthivores while restricting the piscivores. Light extinction coefficients in the 1972–77 period rose to extremes of over $3.0 \cdot m^{-1}$ in summer and fall (Millard and Johnson 1986) which may have adversely affected sight-feeding piscivores such as bowfin (*Amia calva*) and northern pike (*Esox lucius*).

The Bay of Quinte After Phosphorus Control

The substantial decrease of phosphorus inputs to the bay began early in 1978 and rapidly resulted in several significant changes as recorded in 1978–82 (Table 1). Total phosphorus concentrations were reduced in most areas of the bay, with the largest reductions in the upper bay. The degree of phosphorus reduction in the bay is dependent upon the size of the surface sediment pool which will cause lags in the response to point-source control (Minns 1986a).

Primary production rate and phytoplankton biomass dropped significantly soon after point-source phosphorus control became effective (Millard and Johnson 1986; Nicholls et al. 1986). Water quality at the Belleville Filtration Plant improved significantly after phosphorus inputs were reduced (Nicholls et al. 1986). Small, unicellular phytoplankton, cryptomonads and chrysomonads, increased in relative importance, and the growth periods of bloom-forming phytoplankton decreased when phosphorus inputs were reduced.

Alterations in the phytoplankton community apparently did not significantly alter the zooplankton community (Cooley et al. 1986). The macrozooplankton continued to be dominated by the small cladocerans *Bosmina longirostris*, *Eubosmina coregoni*, and *Chydorus sphaericus* (Cooley et al. 1986). *Chydorus sphaericus*, which can feed on blue-green algae, declined at Belleville as the blue-green algae biomass declined there, but increased at Napanee in spite of lower blue-green algae biomass (Cooley et al. 1986). Some larger zooplankton forms, notably *Daphnia galeata mendotae*, showed some increase in abundance following reductions in phosphorus inputs, but their biomass is still minor in relation to the species of small cladocerans.

The macrobenthos populations responded to changing nutrient concentrations and alterations in predator abundance. *Pontoporeia hoyi* abundance increased particularly after 1977 and peaked in 1982 and 1983. Although their numbers dropped 25% in 1984 compared with 1983, their abundance was still high compared with 1972 (Johnson and McNeil 1986). The increase in *Pontoporeia hoyi* can be related to the decreased predation pressure upon them when the white perch (*Morone americana*) collapsed in 1978 (Hurley 1986a). The numbers of

Pontoporeia hoyi may have become excessive in 1982 and 1983, but other fish species such as yellow perch (*Perca flavescens*) and trout-perch (*Percopsis omiscomaycus*) increased in abundance and consumed amphipods (Hurley 1986b; Scott and Crossman 1973).

The decrease in phytoplankton density recorded from 1978 through 1981 may have caused the general decrease in macrobenthos recorded after 1977 (Johnson and McNeil 1986). The biomass of oligochaetes, sphaerids, and *Asellus racovitzai* all decreased, but chironomids remained fairly constant during this period. Predation by yellow perch on *Gammarus fasciatus* may have been important in reducing the numbers of this species after 1978 (Hurley 1986b; Johnson and McNeil 1986).

Macrophytes were relatively little affected by reducing phosphorus inputs despite the increase in depth of the euphotic zone by approximately 0.7 m in the years after phosphorus reductions (Millard 1986). Macrophyte beds act as nutrient traps, but also show seasonal cycling. This cycling may be keeping levels of phosphorus sufficiently high, at least in early spring, to promote greater growth of phytoplankton in those areas at that time, and thus prevent improvements in water transparency (Millard and Johnson 1986). Macrophyte standing crop in the bay was generally low (1972–82 weighted mean, 25.8 g dry weight · m^{-2}) compared with Lake Opinicon, a mesotrophic lake in the same vicinity (248 g dry weight · m^{-2}) (Crowder and Bristow 1986).

The most significant change observed in the fish community was the increase in growth rates of individual species that occurred in 1978 and subsequent years (Christie and Scott 1985; Hurley 1986a). A climate-related crash of white perch populations occurred in the winter of 1977–78 which resulted in an increased growth rate of the remaining white perch (Minns and Hurley 1986). Strong walleye (*Stizostedion vitreum vitreum*) year-classes developed in 1977, and especially in 1978. It is our contention that these year-classes developed because of the reduced predation pressure on walleye fry once white perch numbers were drastically reduced. The subsequent increase in piscivore biomass resulted in a cropping of small benthivores and planktivores. The reduction in benthivores freed invertebrate food reserves for other species so that interspecific competition was relaxed. Increased growth rates of white perch resulted in their reaching the size where they became piscivores, and as a result, the piscivore biomass in the bay doubled (Christie and Scott 1985).

The reactions at the various trophic levels showed that although predation limited the planktivorous and benthivorous fish, the planktivorous fish were unable to exert a significant impact on small herbivorous zooplankton. These small herbivores were extremely abundant, presumably because of the high phytoplankton density. Phytoplankton densities were apparently controlled by nutrient concentrations in the bay, and not by grazing.

Comparison of the Bay of Quinte with Similar Embayments Elsewhere in the Great Lakes

Several areas in the Great Lakes Basin have been subjected to eutrophication and other stresses which match, in some degree, that observed in the Bay of Quinte. Saginaw Bay on Lake Huron and the western basin of Lake Erie have both received high inputs of phosphorus and their biota have also changed dramatically. Oneida Lake is somewhat smaller than the Bay of Quinte and has only an indirect connection to larger lakes. Phosphorus concentrations have increased to some degree in Oneida Lake. West Lake is relatively close to the Bay of Quinte and, because it has not received nutrient loads that are comparable with the bay, was used as a standard by which to compare some of the parameters studied during Project Quinte.

The physical dimensions of each water body show wide diversity; however, the mean depth, especially of the most eutrophic areas, was less than 8 m (Table 2). The number of days required for flushing was least in the Bay of Quinte and greatest in western Lake Erie. No data are available for West Lake, but a cursory examination of its features would place its time for complete flushing considerably higher than the Bay of Quinte.

Total phosphorus concentration and loading were high in the Bay of Quinte during the entire study period relative to the other areas from which data are available. Concentration of chlorophyll *a* was high in the Bay of Quinte, western Lake Erie, and Saginaw Bay but was low in West Lake. The photosynthetic rate was highest in the upper Bay of Quinte, and even in the lower bay, values were relatively high compared with western Lake Erie and Saginaw Bay.

Phytoplankton biomass in the Bay of Quinte in the years before phosphorus control matched values observed in western Lake Erie and Saginaw Bay. A significant reduction in phytoplankton biomass was recorded after phosphorus control in the Bay of Quinte. These values were less than those in western Lake Erie and Saginaw Bay. The lowest phytoplankton biomass was recorded at West Lake. The method of measurement of phytoplankton in Oneida Lake makes comparison with the other areas difficult. But, since Forney (1977) placed the lake between meso- and eutrophic, it is likely that phytoplankton biomass probably lies between that found in West Lake and the other areas.

Phytoplankton composition in West Lake was markedly different from that recorded in three of the other areas. No data were available from Oneida Lake. The biomass of bloom-forming blue-green algae in the upper Bay of Quinte was 20 times that recorded in West Lake. Cryptomonads, dinoflagellates, chrysophytes, and chlorophytes were found in higher proportions in West Lake compared with the Bay of Quinte.

Zooplankton in both the Bay of Quinte and western Lake Erie were dominated by cladocerans. Mean seasonal values for cladocerans in the Bay of Quinte matched closely the maximum values recorded in western Lake Erie but were twice those recorded in Oneida Lake. Small cladocerans such as *Bosmina longirostris*, *Eubosmina coregoni*, and *Chydorus sphaericus* were the major forms in the Bay of Quinte. *Chydorus* was the dominant cladoceran in Oneida Lake. Both cyclopoid and calanoid copepods were less abundant on a mean seasonal basis in the Bay of Quinte than they were in western Lake Erie as determined by their maximum abundance.

Macrophyte distribution and abundance was limited in the Bay of Quinte to under 2 m of water depth in the upper bay. Rooted submergents declined dramatically in Oneida Lake as the result of water level controls imposed in the 1950s. West Lake contained a luxurient macrophyte population with 26 species recorded in depths to 3 m.

Macrobenthos changes have been dramatic in western Lake Erie with the loss of *Hexagenia* in the 1950s being particularly important. This species has been particularly sensitive to increased eutrophy, and has declined when dissolved oxygen in bottom waters became depleted through biological oxidation processes (Britt 1955).

Standing stocks of benthic macroinvertebrates were generally low in the upper Bay of Quinte compared with the lower bay.

TABLE 2. Characteristics of water bodies subjected to various levels of eutrophication (Sources: Cook and Johnson (1974); Eshenroder (1977); Forney (1977); Hartman (1972); Johnson and McNeil (1986); Leach and Nepszy (1976); Mills et al. (1978); Munawar and Munawar (1976); Schneider et al. (1969); Stoermer and Theriot (1985); Vollenweider et al. (1974); Watson (1976)).

	Bay of Quinte	Western Lake Erie	Saginaw Bay	West Lake	Oneida Lake
Drainage basin (km^2)	18200		21000		
Length (km)	64	80.5	82	6.4	33.6
Width (km)	0.8–5.6	64.4	42 (mouth)	6.4	8.8
Area (km^2)	254	3276	2960	20.4	207
Mean depth (m)	3.2 (upper) 23.8 (lower)	7.4	4.6 (inner) 15.6 (outer)	2.8	6.8
Volume (km^3)	2.3	24.2	27		
Flushing rate (d)	40–75	920	186		235
Total dissolved solids (mg · L^{-1})		140 (1900s) 150 (mid-1930s) 200 (early 1970s)	287 (1965) 230 (1970) 204 (1975)		163
Mean total phosphorus (μg · L^{-1})	19–78 (1972–77) 17–48 (1978–81)			14–32	
Phosphorus loading (g · m^{-2} · yr^{-1})	1.47 (prior to 1978) 1.25 (since 1978)	1.07			0.72
Mean Secchi depth (m)	1.2–3.4			2.2–2.6	2.4–3.0
Chlorophyll *a* corrected (mg · m^{-3})	6.5–29.3 (1972–77) 4.4–19.8 (1978–81)	3.3–19.3	9.5–27.4	2.3–5.4	
Photosynthetic rate (mg C · m^{-3} · h^{-1})	Upper bay 124–246 (1972–76) Lower bay 37–91 (1972–76)	4.8–146.9	4.1–127.2		
Phytoplankton	2.0–13.1 g · m^{-3} (1972–77) 1.5–6.6 g · m^{-3} (1978–81) *Melosira*, *Stephanodiscus*, *Anabaena*, *Aphanizomenon*, dominant forms	0.8–13.2 g · m^{-3} (1970); *Aphanizomenon*, *Anabaena*, *Coscinodiscus*, *Octoinastrum*, *Ceratium* typical species	1.6–17.3 g · m^{-3}	0.66 g · m^{-3} *Melosira* less than 10% of total, non-blooming blue-greens form 10%, more diverse types	May–October 1000–100000 cells · mL^{-1}
Zooplankton	Mean seasonal abundance (L^{-1})	Cladocerans (max) 200 · L^{-1} (July 1970)			1964–74
Upper–middle bay	1975–76 / 1979–81 Cladocerans 186 / 149 Cyclopoid copepods 52 / 48 Cananoid copepods 2 / 2	Cyclopoid copepods (max) 100 · L^{-1} (June 1970) Calanoid copepods (max) 30 · L^{-1} (June 1970)			*Chydorus* up to 44 · L^{-1} *Diaptomus* 5–25 · L^{-1} *Daphnia retrocurva* 0–14 · L^{-1} *Daphnia galeata mendata* 4.7 · L^{-1} up to 1969 < 1 · L^{-1} 1970–74 *Daphnia pulex 0 to 1968*, 1968–74, 1–8 · L^{-1}
Lower bay	1975–76 / 1978–81 Cladocerans 47 / 81 Cyclopoid copepods 26 / 50 Cananoid copepods 2 / 3				

TABLE 2. (concluded)

	Bay of Quinte	Western Lake Erie	Saginaw Bay	West Lake	Oneida Lake
Macrophytes	In upper bay, standing crop, species richness and cover low in 1972–82. *Myriophyllum spicatum* dominant			Widely distributed to depths 2–3 m. 26 species found	Rooted submergents declined in 1940s, then abundant in 1965 and more so in mid-1970s 1916: *Potamogeton* 45.5% *Vallisneria* 22.4% *Myriophyllum* 20.9% *Najas* 16.4% 1967: *Vallisneria* 60.4% *Heteranthera* 56.7% *Anacharis* 50.0% *Myriophyllum* 39.6%
Macrobenthos	Standing stock, August 1967–84 84 ash-free dry weight: Upper bay: $1.0 \text{ g} \cdot \text{m}^{-2}$ Lower bay: $3.9 \text{ g} \cdot \text{m}^{-2}$	1928–30, $1150 \cdot \text{m}^{-2}$ 60% oligochaetes 12% *Hexagenia* 25% molluscs 1961, $6930 \cdot \text{m}^{-2}$ 80% oligochaetes 4.6% chironomids 6.3% sphaerids 3.2% gastropods Loss of *Hexagenia* in late 1950s due to O_2 depletion	Oligochaetes and chironomids dominate, decreases in *Hexagenia* and fingernail clams in 1955–1956. Fingernail clams returned by 1965. Average standing crop in 1956 was 4.43 g wet weight $\cdot \text{m}^{-2}$		Ephemeroptera and Trichoptera common in 1917, but not in 1967 and tubificids increased. *Hexagenia* extinct by 1967. Shoreline modifications and climatic events major influences
Fish	Collapse of lake herring in 1940s, loss of lake whitefish, walleye in 1960s, rise of white perch in 1960s. Alewife, white perch dominate to 1970s when white perch decimated. Yellow perch increasing in 1980s, walleye returning in late 1970s and 1980s	Loss of many species in past 150 yr but production consistent and now primarily yellow perch, white bass. Walleye decline linked to changes in environment and growing smelt population	Walleye lost in 1940s. Smelt and alewife proliferate in 1950s. Yellow perch fished heavily since 1940s and population was large. Now showing signs of overfishing	Change in species composition, 1969–76, 4% piscivores, walleye important, 1981–83, 2% piscivores, white perch doubled in number, walleye decline	Catch in 1928, 11–13 $\text{kg} \cdot \text{ha}^{-1}$ In 1957–59, $9.6 \text{ kg} \cdot \text{ha}^{-1}$. American eel and esocids declined in 1920s and 1930s. Walleye numbers increased and depend on yellow perch and lesser on white perch for prey. Growth and survival of walleye depends on year-class strength of yellow perch

TABLE 3. Mean seasonal (May–October) biomass of macrozooplankton of 10 μg · individual^{-1} and greater (dry weight) from three areas of the Bay of Quinte, 1975–84 (nd denotes no data).

Year	Biomass (mg dry weight · m^{-3}) Upper bay	Middle bay	Lower bay
1975	7.31	5.01	3.06
1976	8.19	4.48	1.60
1979	19.57	11.48	7.48
1980	55.45	44.58	4.60
1981	12.74	19.02	1.01
1982	84.48	nd	6.59
1983	36.54	nd	4.24
1984	16.53	nd	3.08

Average standing crop in Saginaw Bay, assuming an 80% loss on conversion to ash-free dry weight, was 0.9 g · m^{-2} in 1956, a value comparable with the upper Bay of Quinte.

The numerical abundance of benthic macroinvertebrates varied markedly between the upper and lower Bay of Quinte. Mean values in August in the upper bay were from less than 1000 to 8000 · m^{-2}, but in the lower bay, values ranged from 2000 to 15 000 · m^{-2} (Johnson and McNeil 1986). These values exceed somewhat those recorded in western Lake Erie. Oligochaetes dominated in the upper Bay of Quinte, while oligochaetes, sphaerids, and amphipods were the major forms in the lower bay. The species composition in the lower bay closely resembled that found in western Lake Erie.

Fish stocks in all the areas have undergone significant and generally unwelcomed changes. In all cases where eutrophication has increased, there has been a decline in large piscivore biomass and a proliferation of planktivores and benthivores. In some cases, such as the Bay of Quinte, western Lake Erie, and Saginaw Bay, other less valued fish stocks were exploited. In each case while the production of fish biomass has not diminished, the value of the harvest has. In Oneida Lake, three of the four major piscivores declined but the remaining walleye increased in abundance (Forney 1977). In West Lake, recent evidence points to a reduction in large piscivores and an increase in the benthivore population.

Ecological Theory and Project Quinte

Project Quinte can be viewed as a test of the experimental management principle as defined by Loftus et al. (1978). The main question to be answered was: Can the damaged ecosystem of the Bay of Quinte be rehabilitated by reducing the point-source inputs of phosphorus? Linked to this question there were ancillary questions concerning the effect of internal regeneration of phosphorus driving species shifts, the effect of climate variations in producing changes in rate functions, and the possibility that certain triggering mechanisms were necessary to produce major changes in species composition. Some of these questions have been addressed by authors reporting in this volume.

The results of Project Quinte can also be used to test some general ecological theories. Do the changes noted in the Bay of Quinte resulting from phosphorus control support the hypothesis that nutrient enrichment is primarily responsible for alterations in species composition and abundance at all trophic levels? Or, do these changes support the hypothesis that predator–prey interactions set the rate at which alterations in community structure at all trophic levels occur, and that nutrient concentrations set the point on a horizontal axis at which these rates commence? Or, do these changes support the hypothesis that phosphorus acts on the community as a stress that alters the steady state at each trophic level to a point where a catastrophic alteration occurs at one or more levels? Rehabilitation resulting from phosphorus reductions would traverse somewhat different courses depending upon which theory is supported.

Nutrient Hypothesis

The nutrient hypothesis suggests that reductions in phytoplankton abundance should occur quickly when phosphorus inputs are reduced. With a rise in the N:P ratio there should be a shift from bloom-forming blue-green algae to Cryptophyceae and Chrysophyceae. A reduction in blue-green algae would increase the proportion of phytoplankton that are of more use in the food chain. This would favour the filter-feeding zooplankton and, presumably, also favour the production of the larger herbivorous forms. Larger zooplankton forms would presumably be preferred food for planktivores and planktivorous stages of other fish species. Ultimately, this process should enhance production and biomass of all fish species. The rate of occurrence of these changes would directly depend on the turnover rates of the organisms involved.

There is ample evidence that phytoplankton biomass and species composition in the Bay of Quinte are dependent on phosphorus concentration (Nicholls et al. 1986). There is also strong evidence that waters of the upper bay were nitrogen limited, as evidenced by the low N:P ratios and presence of nitrogen-fixing phytoplankton (Nicholls and Carney 1986). This occurred because of the high phosphorus loading. Reducing phosphorus inputs resulted in a significant reduction in phytoplankton biomass. There was a decline of nitrogen-fixing blue-green algae and an increase in an assemblage that is more phosphorus limited. The rise of the N:P ratio in the upper bay occurred quickly, largely due to the low residence time of the water mass (Minns 1986b).

Comparison of the Bay of Quinte with West Lake showed that the regressions of concentrations of chlorophyll *a* on total phosphorus had slopes that were not significantly different (F = 0.55, df = 1, 9) but elevations that were significantly different (F = 60.11, df = 1, 10). Chlorophyll *a* levels in West Lake were below those expected on the basis of the relationship derived by Dillon and Rigler (1974). Although Nicholls and Dillon (1978) showed considerable variation in the published phosphorus–chlorophyll relationships, the fact that the time of sampling and methods of analysis were the same for the two areas studied here tends to confirm that the differences were real.

The ratio of chlorophyll *a* to total phosphorus was 0.21 in West Lake, but 0.51 in the Bay of Quinte. This may be the result of the different composition of phytoplankton in the two areas. As stated earlier, bloom-forming blue-green algae comprised 20 times the biomass in the upper Bay of Quinte compared with West Lake. Those types that are typical of oligotrophic systems, such as nonblooming blue-green algae, cryptomonads, dinoflagellates, chrysomonads, and chlorophytes, were all more abundant in West Lake compared with the Bay of Quinte.

The mean seasonal biomass of larger zooplankton, over 10 μg dry weight · individual^{-1}, was calculated for the three areas of the Bay of Quinte in the periods before and after phosphorus control (Table 3). The data in the 1979–84 period are highly variable such that the comparison of the combined upper–middle bay before and after phosphorus control just failed to be significantly different (t = 2.15, df = 11). However, the trend to greater biomass of larger zooplankton after phosphorus control appears established in the upper–middle bay, but is not evident in the lower bay.

Unfortunately, we have no data on the zooplankton composition of West Lake. However, for the Bay of Quinte it appears that a sufficient biomass of larger sized zooplankton has not developed that would impact significantly on phytoplankton biomass and thus on chlorophyll a concentrations.

The nutrient hypothesis explains the observed reduction in phytoplankton biomass but not its composition. A significant shift in the dominance of specific phytoplankton species is not expected to occur until the N:P ratio approaches 30 (Nicholls and Carney 1986). Values of N:P in West Lake ranged from 17.5 to 40.7 with a mean of 28.8, while the Bay of Quinte readings ranged from 11.0 at Belleville to 24.4 at Conway in the whole 1972–81 period.

Although the total biomass of nitrogen-fixing blue-green algae decreased in the years after phosphorus control, their proportion of the total phytoplankton biomass increased (Nicholls et al. 1986). This occurred because phosphorus control had more impact on the diatoms (Bacillariophyceae) than on the blue-green algae so that blue-green algae assumed a greater relative importance (Nicholls et al. 1986).

Predation Hypothesis

If the predation hypothesis is supported, then rehabilitation of the bay would begin only when an alteration in the fish community structure occurred. This alteration would set in motion a chain of interlocking events that ultimately would reach the phytoplankton. By a fortuitous coincidence, a climate-related fish kill occurred in the bay in the same year that phosphorus reductions began. We were presented, therefore, with a natural manipulation of the food web at higher trophic levels. The development of a large piscivorous population in the same year completed the other section of the "biomanipulation" experiment (Shapiro and Wright 1984).

The subsequent alterations in the fish community appear related to the rise of the piscivore biomass in the bay (Christie and Scott 1985; Hurley 1986a). The expected increase in larger zooplankton forms and reduction in the biomass of smaller cladocerans resulting from reduced planktivore abundance has not occurred. Phytoplankton biomass was not further depressed below the levels resulting from the control of phosphorus loading. N:P ratios are still relatively low even though they are increasing, and the chlorphyll a – total phosphorus relationship remains above that predicted by the Dillon–Rigler (1974) model.

However, there is evidence of the far-reaching effects of predator–prey relationships in establishing species composition and abundance in the bay. Since much of the effect at each trophic level is mediated by the effect on the trophic level above it, this has been termed consumer-controlled regulation (McQueen et al. 1985).

Not only are there direct predator–prey relationships, but changes in growth rates of various organisms occur that result from changes in food resources. These shifts in growth rate alter the time at which a predator preys on particular items. This effect is especially important among fish species which display ontogenetic niche shifts. Werner (1984) described how the growth trajectory can be altered by shifts in the foraging efficiency of a fish species. Because mortality and reproduction schedules are altered by growth characteristics, the population dynamics of a species are profoundly affected by alterations in the growth rate (Christie and Scott 1985).

These authors proposed that stunting occurred among species of fish in the bay because of competition that resulted from insufficient numbers of piscivores to crop young fish. They plotted production per fish against the mean biomass in the fish community and found a family of lines which produced a sigmoid curve. In a community where piscivores are plentiful, both net production and mean fish weight are high. With reducing piscivore abundance, net production and mean fish biomass fall quickly. The health of a fish community can be assessed by these criteria.

To test this hypothesis, the number of fish in weight classes with midpoints from 1.8 to 562.3 g was determined using data from bottom trawl drags in the Bay of Quinte as described by Hurley (1986a). The numbers of fish in the upper bay of all species vulnerable to the bottom trawl and less than 18 g in weight were compared in the 1972–77 and 1978–84 periods. This number fell from between 30 and 93% in the years 1978–84 when piscivore abundance increased compared with the 1972–77 period. The exceptions to this were in 1979 and 1981 when large numbers of young-of-the-year alewives (*Alosa pseudoharengus*) and white perch were taken in July and August. Similarly, the numbers of fish less than 18 g in the middle bay decreased from between 52 and 94% in the years 1978–84 compared with the 1972–77 period. In the lower bay, however, there was an overall increase of 6% in the numbers of fish under 18 g in weight in the 1978–84 period. Piscivore abundance in the lower bay was not as great as in the upper and middle bay, and small alewives and rainbow smelt (*Osmerus mordax*) were very abundant in the lower bay (Hurley 1986a).

The reduction in the numbers of small-sized fish had a noticeable effect on the biomass of macrozooplankton (> 10 μg dry weight · individual^{-1}) in the upper bay in the 1979–84 period. In two years, 1979 and 1981, when macrozooplankton biomass was low in the upper bay (Table 3), the number of small fish was high. The regression equation that described the entire 1979–84 period was as follows:

$$\log_{10} \text{macrozooplankton } (\text{mg} \cdot \text{m}^{-3}) = 2.914 - 0.551 \log_{10} \text{trawl catch per unit effort of fish 18 g and under}, P < 0.05.$$

A cautionary note must be sounded here, since many small-sized fish would not be vulnerable to the trawl and their numbers would, therefore, be underestimated. Minns and Hurley (1986) discuss the possible magnitude of the underestimate in regard to white perch.

The relationship between alewife biomass and macrozooplankton biomass (both wet weight) was significant in both the upper–middle and lower bay, unlike the phenomenon described above which was significant only in the upper bay. For the upper-middle bay the regression was

$$\log_{10} \text{macrozooplankton biomass } (\text{mg} \cdot \text{L}^{-1}) = -0.705 - 0.568 \log_{10} \text{alewife biomass } (\text{mg} \cdot \text{L}^{-1}), P < 0.005$$

and for the lower bay the regression was

$$\log_{10} \text{macrozooplankton biomass } (\text{mg} \cdot \text{L}^{-1}) = -1.689 - 0.334 \log_{10} \text{alewife biomass } (\text{mg} \cdot \text{L}^{-1}), P < 0.025.$$

Comparison of these two regressions showed that the regression coefficients were not significantly different (F = 1.40, df = 1, 17) but the elevations were significantly different (F = 55.51, df = 1, 18, $P < 0.001$). This difference in elevation is related to the smaller concentration of macrozooplankton in the lower bay compared with the upper–middle bay (Table 3).

Macrozooplankton are preferred diet items for several fish species examined in the Bay of Quinte (Hurley 1986b). Alewives are planktivorous throughout their lives. In the upper bay, white perch up to 100 mm fork length and yellow perch up to 80 mm fork length depend to a substantial degree (35 to 76% of total diet biomass) on macrozooplankton. White perch at 100 mm fork length weigh about 15 g, while yellow perch at 80 mm fork length weigh about 8 g (Christie and Scott 1985).

The presence of large numbers of alewives and rainbow smelt in the lower bay (Hurley 1986a) is probably responsible for the relatively small biomass of macrozooplankton recorded there (Table 3). The diet of rainbow smelt up to 14 g consisted of 67–99% cladocerans and copepods (D.A. Hurley, unpubl. data). The abundance of young-of-the-year rainbow smelt increased markedly in the lower bay after 1974 (Hurley 1986a).

It is significant that a reduction in the number of small-sized fish in the upper–middle bay that was observed when piscivores increased has apparently resulted in an increase in macrozooplankton. It would be expected that these forms, some of which are predaceous on microzooplankton, would result in a decrease in the abundance of microzooplankton. Up to 1984, however, this has not occurred.

Succession Hypothesis

In the case of the succession hypothesis, we would expect dramatic shifts, especially at the phytoplankton–zooplankton interface, only when a significant alteration in phosphorus inputs occurred that would overcome the resistance to shift to a new level. Although we have observed some alterations in phytoplankton abundance, it is possible that phosphorus regeneration from the bottom sediments, together with the nonlinear relationship between productivity and nutrient loading (Millard 1986), is maintaining the system at its present level.

By Odum's (1969) criteria of developmental and mature ecosystems, the Bay of Quinte is in the developmental stages. However, contrary to the prediction of the succession hypothesis, the growth rates of several fish species declined as nutrient enrichment increased. The reproductive potential of these species remained high because sexual maturity occurred at smaller sizes. The total production of these species, however, did not increase as nutrient enrichment and other alterations reduced the piscivore biomass. Growth, longevity, maturation, and reproduction apparently compensate to maintain a fairly steady biomass.

A successional model for the Bay of Quinte may be viewed as containing several step-functions, or cusps, in which the mean size of the organisms in the system and their generation time are dependent upon particular levels of nutrient inputs (Minns et al. 1986). Relatively high resistance to change in the step-function is evident until the critical point is reached. After that point, the system collapses to a new level and the process continues. The model views the collapses of piscivores and the decreasing size of their prey, the loss of large zooplankton, and the proliferation of bloom-forming blue-green algae as successional stages in the degradation process. The return to a more mature system will reverse the process, but the length of time required at each stage is not known.

The evidence obtained from Project Quinte to the early 1980s lends support to both the nutrient hypothesis and the predation hypothesis. The succession hypothesis does not appear to be supported. However, the lack of data to support this hypothesis may be a function of continued release of phosphorus from the sediment pool which is suppressing the rehabilitation process (Minns 1986b).

The Size-Spectrum Model of Biomass

Minns et al. (1985) used the model of Borgmann (1982, 1985) to link nutrients with biomass and production at various trophic levels in the Bay of Quinte. Project Quinte data used in this model show a reduced transfer of production along the size-spectrum from phytoplankton to large fish. It appears that the decreased transfer efficiency has produced less biomass at larger size ranges, and that this decrease is a result of eutrophication.

The evidence of large biomass of small-sized fish obtained in bottom trawl drags discussed earlier confirms this prediction. This model also suggests that zooplankton biomass is not being controlled by predation. The numerical abundance of small zooplankton species in the bay even after phosphorus control is consistent with the hypothesis. The model also predicts that phytoplankton biomass is depressed because of the heavy zooplankton grazing and not because of nutrient restriction. The trend toward increased size of zooplankton may result in a more efficient use of phytoplankton, while the continued reduction in total phosphorus concentration may favour the more "food-chain" functional forms of phytoplankton. By this model, it is evident that alterations so far observed in the bay have not reached the critical phytoplankton–zooplankton interaction. This model appears to link the nutrient and predation hypotheses so that the deficiencies of each are overcome.

General Comments

There is little doubt that phosphorus reduction produced the initial reaction in phytoplankton biomass that resulted in improved water clarity and possibly increased the effectiveness of sight-feeding predators. Predator–prey interactions have been effective at the higher trophic levels and have resulted in a decrease in the mean number of small-sized fish. A relaxation of predation on larger zooplankton has resulted in an increase in their number in the upper bay. However, these increases have yet to impact significantly on the phytoplankton to alter species composition in a major way.

Biomanipulation experiments as described by Benndorf et al. (1984) and Shapiro and Wright (1984) have involved reductions in planktivores and benthivores and additions of piscivores in a small lake (12.6 ha) or pond (0.044 ha). Reactions at the various trophic levels in these experiments were evident within 2 yr. It would be expected in an area such as the Bay of Quinte that covers 25 364 ha that a longer period of time would be required before all the changes imposed by biomanipulation would occur.

Recently, Pace (1984) examined the zooplankton community structure in relation to phytoplankton biomass in lakes ranging from 130 to 5610 ha and concluded that the relationship between zooplankton size and phytoplankton biomass was weak. He suggested that dramatic reductions in phytoplankton biomass by manipulation of the food web probably require radical changes, such as large-scale fish kills, to be effective. He questioned whether these changes would be stable.

Perhaps the most significant finding was that lakes with higher ratios of macro- to microzooplankton have less chlorophyll *a* per unit of total phosphorus (Pace 1984). In the Bay of Quinte the ratio of macro- to microzooplankton is not sufficiently great to impact on the chlorophyll *a* – total phosphorus relationship. Unfortunately, we have no data on the zooplankton composition of West Lake by which we could further test this hypothesis.

Implications for Management

One of the key elements in the strategy for Ontario fisheries is the establishment of adequate trend-through-time data series from which the adaptive or experimental management of fisheries can be based (Loftus et al. 1978). Project Quinte formed a trend-through-time series in which we could compare and contrast data from both within the Bay of Quinte and between it and other water bodies in the Great Lakes. These data can be used to formulate and test hypotheses, to adapt the study technique, and to offer predictions about rehabilitation of damaged ecosystems.

It is evident that the Bay of Quinte has shown numerous signs of rehabilitation, but it is not in a steady state. Data presented in papers in this volume and summarized here show trends in phytoplankton biomass and species composition, in zooplankton size composition, in macrobenthos composition and biomass, and in fish species shifts that are in the direction generally regarded as rehabilitative.

Our studies indicate that there are features that can be measured in water bodies, especially in the lower Great Lakes region, that can be used as guides to the overall health of the aquatic ecosystem. The following list describes these measurable features.

(1) A whole-lake phosphorus model was developed which emphasizes the role of reflux and permanent deposition of phosphorus in lake sediments and which predicts the responses of lakes to changing phosphorus loads (Minns 1986a). Annual measurements of the phosphorus concentration in both the sediments and the water column are required to assess the effectiveness of reduced phosphorus loads.

(2) Loadings of phosphorus from point sources and from rivers can be estimated from population size and river gauges (Minns 1986b). Depending upon phosphorus inputs and water residence time, the requirement for sewage treatment will vary, but summer phosphorus concentration should be kept below $50 \text{ mg} \cdot \text{m}^{-3}$ in the Bay of Quinte.

(3) Rising chlorophyll *a* concentration is a clear signal that an ecosystem is adversely affected. This is especially evident when the ratio of chlorophyll *a* to total phosphorus rises above that predicted by the model proposed by Dillon and Rigler (1974) in lakes where the total nitrogen to total phosphorus ratio is greater than 12. By their model the chlorophyll *a* to total phosphorus ratio was 0.35. In the Bay of Quinte it was 0.51, while at West Lake it was 0.21.

(4) Phytoplankton maxima of $30 \text{ mm}^3 \cdot \text{L}^{-1}$ together with week-to-week changes of 100–300% resulting from changes in dominant species are clear indicators of advanced eutrophy (Nicholls et al. 1986). Even after phosphorus control, the mean June–August 1980 value for phytoplankton in the upper bay at Trenton was $5.90 \text{ mm}^3 \cdot \text{L}^{-1}$, while at West Lake the mean value was $0.66 \text{ mm}^3 \cdot \text{L}^{-1}$. By this criterion, therefore, phytoplankton abundance in the upper bay still remains high.

(5) Light limitation of primary production is characteristic of advanced eutrophy. The underwater light regime becomes controlled by chlorophyll *a* concentration and the depth of water mixing. Therefore, the euphotic zone standing crops reach maximum values because the euphotic zone depth decreases as chlorophyll *a* concentrations increase and net photosynthesis becomes limited (Millard 1986).

(6) The food chain acceptability and human use aspects of the phytoplankton community can be assessed from the ratio of the May–October average biomass of Chrysophyceae + Cryptophyceae divided by the average biomass of blue-green bloom-forming species. This index, called the "*F*" value, when it has values $>>1$ reflects a more "desirable" phytoplankton community than values $<<1$ (Nicholls et al. 1986).

(7) The size spectrum of macrozooplankton can be an indicator of the state of an ecosystem. The presence of large numbers of small-sized cladocerans is particularly indicative of stressed systems. Although increasing numbers of larger cladocerans in the Bay of Quinte, such as *Daphnia galeata mendotae* and *Daphnia pulex*, after phosphorus control are encouraging, their proportions to the total macrozooplankton biomass are still small. It is apparent that there are insufficient numbers of large cladocerans in the bay to exert an influence on the ratio of chlorophyll *a* to total phosphorus.

(8) There were increases in species of macrobenthos that are less tolerant of eutrophic conditions, such as *Chironomus atritibia*, *Spirosperma ferox*, and *Stylodrilus heringianus*, after phosphorus control (Johnson and McNeil 1986). There was also a general decline in both numbers and biomass of oligochaetes, sphaerids, and isopods which may be related to a decline in productivity resulting from reduced phosphorus inputs or alterations in the food web.

(9) The abundance of submerged marcophytes decreased dramatically from the 1950s and early 1960s to the late 1960s coinciding with an increase in phytoplankton standing crop (Crowder and Bristow 1986; Nicholls et al. 1986). Standing crop, species richness, and cover were relatively low in the 1972–82 period, especially in the Belleville–Big Bay area. The macrophyte community has not responded to phosphorus reductions into the mid-1980s, and this feature illustrates the continued instability of the ecosystem.

(10) Significant relationships between planktivore biomass and macrozooplankton biomass were developed for the Bay of Quinte which may be more generally applicable. The specific relationship, however, would have to be developed for each water body. To do this it would be necessary first to examine the diet of the major fish species to determine the proportion of each species that are planktivorous. It would also be necessary to determine the species composition and biomass of the zooplankton and the biomass of planktivores. These measurements would be required over a period of several years during which, hopefully, sufficient yearly changes would be recorded to establish a trend.

(11) The rise in piscivore abundance beginning in 1977–78 in the bay resulted in a major alteration in growth rates and abundance of several planktivores and benthivores (Christie and Scott 1985; Hurley 1986a). Although the fish community of the bay is still not stable, evidence indicates that the severe depreciation occurred when piscivore biomass was less than 20% of the total fish biomass. Included in the piscivore biomass are the large obligate species and the proportion of other species that become partially piscivorous at larger sizes. In recent years, 1979–82, piscivore biomass in the Bay of Quinte has ranged from 35 to 57% of the total fish biomass (Hurley 1986a). Planktivore abundance in the upper and middle bay has declined since piscivores have increased but not in the lower bay where piscivores are relatively less abundant. Part of this reduction in planktivore abundance resulted from decreased alewife numbers. However, some of the reduction has resulted from the lowered biomass of the young of other species which, because of increased growth rates, spent less time as planktivores.

To conclude, one of the most important lessons learned from our efforts in Project Quinte was the necessity of an holistic outlook, sometimes called an ecosystem approach. Each of us when studying our relatively specialized areas came to realize that the results of our colleagues in other fields often assisted us in the interpretation of our own results. This realization not only helped us to mature scientifically, but it also impressed upon us the necessity of cross-disciplinary studies in examining broad ecological issues. We trust we learned this lesson well.

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References

Andersson, G. H., Berggren, G. Cronberg, and C. Gelin. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9–15.

Benndorf, J., H. Kneschke, K. Kossatz, and E. Penz. 1984. Manipulation of the pelagic food web by stocking with predacious fishes. Int. Rev. Gesamten Hydrobiol. 69: 407–428.

Borgmann, U. 1982. Particle-size conversion efficiency and total animal production in pelagic ecosystems. Can. J. Fish. Aquat. Sci. 39: 668–674.

1985. Predicting the effect of toxic substances on pelagic ecosystems. Sci. Total Environ. 44: 111–121.

Britt, N. W. 1955. Stratification in western Lake Erie in summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population. Ecology 36: 239–244.

Christie, W. J. 1985. A perspective on the fish and fisheries of Lake Ontario. File report GFS-05-85, Glenora Fisheries Station, Picton, Ont.

Christie, W. J., and K. A. Scott. 1985. A comparison of three warmwater fish communities in the Bay of Quinte area of Lake Ontario. File report GFS-10-83, Glenora Fisheries Station, Picton, Ont.

Cook, D.G., and M.G. Johnson. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 763–782.

Cooley, J. M., J. E. Moore, and W. T. Geiling. 1986. Population dynamics, biomass, and production of the macrozooplankton in the Bay of Quinte during changes in phosphorus loadings. p. 166–176. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Crowder, A., and M. Bristow. 1986. Aquatic macrophytes in the Bay of Quinte, 1972–82, p. 114–127. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Dillon, P. J., and F. H. Rigler. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

Eshenroder, R. L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34: 1830–1838.

Forney, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34: 1812–1820.

Hartman, W. L. 1972. Lake Erie: effects of exploitation, environmental changes, and new species on the fishery resources. J. Fish. Res. Board Can. 29: 899–912.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4: 1–23.

Hrbacek, J., M. Dvorakova, V. Korinek, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verh. Int. Ver. Limnol. 14: 192–195.

Hurley, D. A. 1986a. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control, p. 201–214. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. Effect of nutrient reduction on the diets of four fish species in the Bay of Quinte, Lake Ontario, p. 237–246. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Hurley, D. A., and W. J. Christie. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Johnson, M. G., and R. O. Brinkhurst. 1971. Benthic community metabolism in the Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1715–1725.

Johnson, M. G., and O. C. McNeil. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–84, p. 177–189. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Johnson, M. G., and G. E. Owen. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43 (5): 836–853.

Leach, J. H., and S. J. Nepszy. 1976. The fish community in Lake Erie. J. Fish. Res. Board Can. 33: 622–638.

Loftus, K. H., M. G. Johnson, and H. A. Regier. 1978. Federal–provincial strategic planning for Ontario fisheries: management strategy for the 1980s. J. Fish. Res. Board Can. 35: 916–927.

Lynch, M., and J. Shapiro. 1981. Predation, enrichment and phytoplankton community structure. Limnol. Oceanogr. 26: 86–102.

McQueen, D. J., J. R. Post, and E. L. Mills. 1985. Trophic relationships in freshwater pelagic ecosystems. Manuscript in prep., York University, Toronto, Ont.

Millard, E. S. 1986. Effect of light climate, photosynthetic capacity, and respiration on gross integral primary production and net primary production potential in the Bay of Quinte, Lake Ontario, p. 128–138. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Millard, E. S., and M. G. Johnson. 1986. Effect of decreased phosphorus loading on primary production, chlorophyll *a*, and light extinction in the Bay of Quinte, Lake Ontario, 1972–82, p. 100–113. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Mills, E. L., J. L. Forney, M. D. Clady, and W. R. Schoffner. 1978. Oneida Lake. *In* J. A. Bloomfield [ed.] Lakes of New York State. Academic Press, New York, NY.

Minns, C. K. 1986a. A simple whole-lake phosphorus model and a trial application to the Bay of Quinte, p. 84–90. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

1986b. Total phosphorus loading in the Bay of Quinte between the years 1800 and 2000: a model study, p. 77–83. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K. and D. A. Hurley. 1986. Population dynamics and production of white perch, *Morone americana*, in the Bay of Quinte, Lake Ontario, p. 215–223. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Minns, C. K., E. S. Millard, J. M. Cooley, M. G. Johnson, D. A. Hurley, K. H. Nicholls, G. W. Robinson, G. E. Owen, and A. A. Crowder. 1985. Production and biomass size-spectra in the Bay of Quinte, an eutrophic ecosystem. Manuscript, G.L.F.R.B., Burlington, Ont.

Minns, C. K., G. E. Owen, and M. G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965–81, p. 59–76. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Munawar, M., and I. F. Munawar. 1976. A lakewide study of phytoplankton biomass and its species composition in Lake Erie, April–December 1970. J. Fish. Res. Board Can. 33: 581–600.

Nicholls, K. H., and E. C. Carney. 1986. Nitrogen and phosphorus limitation to phytoplankton in the Bay of Quinte and implications for phosphorus loading controls, p. 139–144. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Nicholls, K. H., and P. J. Dillon. 1978. An evaluation of phosphorus–chlorophyll–phytoplankton relationships for lakes. Int. Rev. Gesamten Hydrobiol. 63: 141–154.

Nicholls, K. H., L. Heintsch, E. Carney, J. Beaver, and D. Middleton. 1986. Some effects of phosphorus loading reductions on phytoplankton in the Bay of Quinte, Lake Ontario, p. 145–158. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Odum, E. P. 1969. The strategy of ecosystem development. Science (Wash., DC) 164: 262–270.

Pace, M. L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus–chlorophyll *a* relationship. Can. J. Fish. Aquat. Sci. 41: 1089–1096.

Reinertsen, J., and Y. Olsen. 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. Verh. Int. Ver. Limnol. 22: 649–657.

Schneider, J. C., F. F. Hooper, and A. M. Beeton. 1969. The distribution and abundance of benthic fauna in Saginaw Bay, Lake Huron. Proc. 12th Conf. Great Lakes Res. 1969: 80–90.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation — an ecosystem approach to lake restoration. Contribution No. 143 from Limnological Research Center, University of Minnesota. Mimeographed. 32 p.

Shapiro, J., and D. I. Wright. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwater Biol. 14: 371–383.

Sly, P. G. 1986. Review of post-glacial changes and cultural impacts in the Bay of Quinte, p. 7–26. *In* C. K. Minns, D. A. Hurley, and K. H. Nicholls [ed.] Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86: 270 p.

Stoermer, E. F., and E. Theriot. 1985. Phytoplankton distribution in Saginaw Bay. J. Great Lakes Res. 11: 132–142.

Stoermer, E. F., J. A. Wolin, C. L. Schelske, and D. J. Conley. 1985. Postsettlement diatom succession in the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. 42: 754–767.

Vollenweider, R. A., M. Munawar, and P. Stadelmann. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Board Can. 31: 739–762.

Warwick, W. F. 1980. Palaeolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 117 p.

Watson, N. H. F. 1976. Seasonal distribution and abundance of crustacean zooplankton in Lake Erie, 1970. J. Fish. Res. Board Can. 33: 612–621.

Werner, E. E. 1984. The mechanisms of species interactions and community organization in fish. *In* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle [ed.] Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, NJ.